Chapter 10

BIODIVERSITY OF HETEROPTERA

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The Heteroptera, or true bugs, currently considered a suborder of the Hemiptera, represent the largest and most diverse group of hemimetabolous insects. Much attention has been devoted to the classification of the Hemiptera in recent years, beginning with the realization that the order Homoptera is paraphyletic, based on both morphological and molecular evidence. As a consequence, a larger, more encompassing order Hemiptera, with the four suborders Auchenorrhyncha, Sternorrhyncha, Coleorrhyncha, and Heteroptera (Wheeler et al. 1993), is currently recognized. Additional studies done more recently now suggest that Auchenorrhyncha is not monophyletic and should be separated into the suborders Fulgoromorpha and Cicadomorpha (Bourgoin and Campbell 2002, Brambila and Hodges 2004). Recent use of the confusing term Prosorrhyncha (e.g., Sorensen et al. 1995, Maw et al. 2000, Schaefer 2003), which includes the Heteroptera and the Coleorrhyncha, has not been widely accepted.

Nevertheless, the suborder Heteroptera is considered a monophyletic group generally defined by the wings lying flat over the body, with the forewings partially sclerotized and partially membranous, a piercing-sucking labium that arises anteriorly on the head, four- to five-segmented antennae, a large well-developed scutellum, paired metathoracic scent glands in adults, and dorsal abdominal scent glands in nymphs, among other specializations (Slater 1982, Schuh and Slater 1995). The Heteroptera are separated into seven infraorders (Štys and Kerzhner 1975), two of which are primarily aquatic (Gerromorpha and Nepomorpha), one semiaquatic (Leptopodomorpha), and the remaining four terrestrial (Enicocephalomorpha, Dipsocoromorpha, Cimicomorpha, and Pentatomomorpha).

With the availability of a number of comprehensive world catalogs, recent estimates of the number of described true bugs have taken on a new level of accuracy. We now have world catalogs for nearly all the major families (e.g., Aradidae, Lygaeoidea, Miridae, Reduviidae, Tingidae). In addition, the appearance of large regional catalogs for North America (Henry and Froeschner 1988), Australia (Cassis and Gross 1995, 2002), and the Palearctic (Aukema and Rieger 1995–2006) has added significant documentation of the world fauna. Catalogs of the last two major groups, the Coreidae (M. Webb, personal communication) and Pentatomidae (D. A. Rider, personal communication), are now well underway. Comprehensive reviews, such as the 'True Bugs of the World' (Schuh and Slater 1995), have provided ready access to additional information on Heteroptera. A recent study on global diversity of the water bugs (Polhemus and Polhemus 2008) raised the aquatic bug numbers considerably. Given these resources, the most recent estimate of the number of described Heteroptera ranges from 38,000 (Schuh and Slater 1995, Schaefer 2003) to 39,300 (Cassis and Gross 1995, 2002). Based on the documentation presented in this chapter and my search of the literature, using Zoological Record (since 1995 for the Enicocephalomorpha to the Cimicomorpha and since 2002 for the Pentatomomorpha), the number of described true bugs is now more than 42,300 (Table 10.1), an increase of more than 3000 species.

The question of how many Heteroptera actually occur on the planet remains conjecture. Speculation on the number of insects present in the world has taken on enormous new proportions in recent years. Figures from 650,000 to 1 million described species given in most textbooks, with bold estimates of 2.5 to 10 million species (e.g., Metcalf 1940, Sabrosky 1952), led most to believe that a minimum of half or more of the taxa had been described. A paper by Erwin (1982) with an estimate of up to 30 million insects globally, based on canopy fogging in Panama, realigned most thinking on insect biodiversity in the world, and since then numerous other papers have appeared offering additional hypotheses, some of which predict 80 million or more species will be discovered (e.g., Stork 1988, Erwin 2004). As more and more areas are explored, particularly some of the designated 'hotspots' (e.g., Mittermeier et al. 2004) revealing huge numbers of new Miridae from Australian (Cassis et al. 2006, G. Cassis and R. T. Schuh, personal communication) and Neotropical forest canopies involving numerous families of Heteroptera taken by T. L. Erwin (T. J. Henry, personal observations), we can expect tremendous increases in the number of species.

In this chapter, I present an overview of the seven infraorders of Heteroptera and all 89 of the currently recognized families. For each family, I provide a brief diagnosis, selected information on their habits and economic importance, references to the key literature, and the known numbers of species. Table 10.1 provides the numbers of genera and species for the Australian, Nearctic, and Palearctic regions compared with the world. In my concluding remarks, I discuss the importance of understanding heteropteran biodiversity from a phylogenetic and economic viewpoint, including their role in conservation biology and global warming.

Table 10.1 Summary of the known number of heteropteran genera and species by family and infraorder for the Australian[1], Nearctic[2], and Palearctic[3] regions and the world[4].

	Australian		Nearctic		Palearctic		World	
Taxon	**Genus**	**Species**	**Genus**	**Species**	**Genus**	**Species**	**Genus**	**Species**
Enicocephalomorpha:								
Aenictopecheidae	2	2	1	1	1	1	10	20
Enicocephalidae	3	5	4	9	6	15	55	405
Total	**5**	**7**	**5**	**10**	**7**	**16**	**65**	**425**
Dipsocoromorpha:								
Ceratocombidae	1	1	1	4	1	11	8	52
Stemmocryptidae	0	0	0	0	0	0	1	1
Dipsocoridae	1	4	1	2	1	14	5	51
Hypsipterygidae	0	0	0	0	0	0	1	4
Schizopteridae	13	61	4	4	6	9	44	229
Total	**15**	**66**	**6**	**10**	**8**	**34**	**59**	**337**
Gerromorpha:								
Gerridae (Gerroidea)	20	113	8	47	20	99	67	751
Hebridae (Hebroidea)	3	8	3	15	4	24	9	221
Hermatobatidae (Gerroidea)	1	2	0	0	1	2	1	9
Hydrometridae (Hydrometroidea)	1	15	1	6	1	14	7	126
Macroveliidae (Hebroidea)	0	0	2	2	0	0	3	3
Mesoveliidae (Mesovelioidae)	4	13	1	3	2	7	12	46
Paraphrynoveliidae (Hebroidea)	0	0	0	0	0	0	1	2
Veliidae (Gerroidea)	20	176	4	31	11	64	61	962
Total	**49**	**327**	**19**	**104**	**39**	**210**	**161**	**2120**
Nepomorpha:								
Aphelocheiridae (Naucoroidea)	1	6	0	0	1	18	1	78
Belostomatidae (Nepoidea)	2	5	3	17	5	14	9	160
Corixidae (Corixoidea)	5	46	18	136	15	143	35	607
Gelastocoridae (Ochteroidea)	1	47	2	7	1	4	3	111
Helotrephidae (Notonectoidea)	1	12	0	0	0	0	21	180
Naucoridae (Naucoroidea)	8	36	4	29	7	9	37	391
Nepidae (Nepoidea)	5	23	3	13	5	21	15	268
Notonectidae (Notonectoidea)	6	92	3	35	4	50	11	400
Ochteridae (Ochteroidea)	2	29	1	6	1	3	3	68
Pleidae (Notonectoidea)	1	6	2	5	2	6	3	38
Potamocoridae (Naucoroidea)	0	0	0	0	0	0	2	8
Total	**32**	**302**	**36**	**248**	**41**	**268**	**140**	**2309**
Leptopodomorpha:								
Aepophilidae (Saldoidea)	0	0	0	0	1	1	1	1
Leptopodidae (Leptopodoidea)	1	4	1	1	4	11	32	39
Omaniidae (Leptopodoidea)	0	1	0	0	2	2	2	6
Saldidae (Saldoidea)	6	23	11	70	14	99	29	335
Total	**7**	**28**	**12**	**71**	**20**	**113**	**64**	**381**
Cimicomorpha:								
Anthocoridae (Cimicoidea)	12	23	20	73	26	170	71	445
Lyctocoridae (Cimicoidea)	1	1	1	8	1	10	1	27
Lasiochilidae (Cimicoidea)	3	5	2	8	1	1	10	62
Cimicidae (Cimicoidea)	1	1	8	15	5	15	24	110
Curaliidae (Velocipedoidea)	0	0	1	1	0	0	1	1
Joppeicidae (Joppeicoidea)	0	0	0	0	1	1	1	1
Medocostidae (Naboidea)	0	0	0	0	0	0	1	1

(continued)

Table 10.1 *(continued).*

	Australian		Nearctic		Palearctic		World	
Taxon	**Genus**	**Species**	**Genus**	**Species**	**Genus**	**Species**	**Genus**	**Species**
Microphysidae (Microphysoidea)	0	0	4	4	3	27	5	25
Miridae (Miroidea)	91	186	223	1930	397	2808	1300	10,400
Nabidae (Naboidea)	7	22	10	34	10	112	31	386
Pachynomidae (Reduvioidea)	0	0	0	0	1	2	4	15
Plokiophilidae (Cimicoidea)	0	0	0	0	0	0	5	13
Polyctenidae (Cimicoidea)	2	2	1	2	2	3	5	32
Reduviidae (Reduvioidea)	100	226	49	184	145	808	981	6878
Thaumastocoridae (Miroidea)	3	11	1	1	0	0	6	19
Tingidae (Miroidea)	56	147	22	154	61	473	260	2124
Velocipedidae (Velocipedoidea)	0	0	0	0	0	0	1	25
Total	**276**	**624**	**342**	**2414**	**653**	**4430**	**2707**	**20,564**
Pentatomomorpha:								
Acanthosomatidae (Pentatomoidea)	17	45	2	4	9	107	46	184
Alydidae (Coreoidea)	7	16	11	30	26	69	45	254
Aphylidae (Pentatomoidea)	2	3	0	0	0	0	2	3
Aradidae (Aradoidea)	38	143	10	123	28	204	233	1931
Artheneidae (Lygaeoidea)	1	2	2	2	4	16	8	20
Berytidae (Lygaeoidea)	6	7	7	12	13	54	36	172
Blissidae (Lygaeoidea)	9	15	3	28	8	55	50	435
Canopidae (Pentatomoidea)	0	0	0	0	0	0	1	8
Colobathristidae (Lygaeoidea)	1	1	0	0	2	7	23	84
Coreidae (Coreoidea)	43	83	33	88	84	306	267	1884
Cymidae (Lygaeoidea)	4	10	2	10	2	17	9	54
Cryptorhamphidae (Lygaeoidea)	2	4	0	0	0	0	2	4
Cydnidae (Pentatomoidea)	21	83	17	84	38	171	120	765
Cyrtocoridae (Pentatomoidea)	0	0	0	0	0	0	4	11
Dinidoridae (Pentatomoidea)	4	6	0	0	4	19	16	65
Geocoridae (Lygaeoidea)			2	28	7	75	25	274
Hyocephalidae (Coreoidea)	2	3	0	0	0	0	2	3
Heterogastridae (Lygaeoidea)	3	5	1	2	11	24	24	100
Henicocoridae (Lygaeoidea)	1	1	0	0	0	0	1	1
Idiostolidae (Idiostoloidea)	2	3	0	0	0	0	3	4
Largidae (Pyrrhocoroidea)	2	4	3	12	3	8	13	106
Lestoniidae (Pentatomoidea)	1	2	0	0	0	0	1	2
Lygaeidae (*sensu stricto*) (Lygaeoidea)	22	81	13	70	29	59	102	968
Malcidae (Lygaeoidea)	0	0	0	0	2	25	3	29
Megarididae (Pentatomoidea)	0	0	0	0	0	0	1	16
Ninidae (Lygaeoidea)	2	2	1	1	2	5	5	13
Oxycarenidae (Lygaeoidea)	1	4	2	10	19	63	23	147
Pachygronthidae (Lygaeoidea)	6	10	3	7	6	17	13	78
Parastrachiidae (Pentatomoidea)	0	0	0	0	0	0	1	2
Pentatomidae (Pentatomoidea)	134	363	60	222	219	841	900	4700
Phloeidae (Pentatomoidea)	0	0	0	0	0	0	2	3
Piesmatidae (Lygaeoidea)	1	4	1	7	2	19	6	44
Plataspidae (Pentatomoidea)	2	20	0	0	10	104	59	560
Pyrrhocoridae (Pyrrhocoroidea)	3	11	2	10	13	43	33	340
Rhopalidae (Coreoidea)	2	6	10	39	14	69	21	209
Rhyparochromidae (Lygaeoidea)	75	185	54	163	135	564	372	1850
Scutelleridae (Pentatomoidea)	10	22	15	34	38	158	81	450
Stenocephalidae (Coreoidea)	1	1	0	0	1	18	1	16
Termitaphidae (Aradoidea)	1	1	0	0	0	0	2	9

Table 10.1 *(continued).*

Taxon	Australian		Nearctic		Palearctic		World	
	Genus	Species	Genus	Species	Genus	Species	Genus	Species
Tessaratomidae (Pentatomoidea)	12	18	1	1	12	30	55	240
Thaumastellidae (Pentatomoidea)	0	0	0	0	1	1	1	3
Urostylididae (Pentatomoidea)	0	0	0	0	8	131	11	170
Total	**438**	**1164**	**255**	**987**	**750**	**3279**	**2623**	**16,211**
Grand Total	**822**	**2518**	**675**	**3844**	**1518**	**8350**	**5819**	**42,347**

[1]Based on Cassis and Gross (1995, 2002).
[2]Based on chapters in Aukema and Rieger (1995–2006).
[3]Based on chapters in Henry and Froeschner (1988).
[4]Based on a summary of all sources cited in this chapter.

The text is arranged phylogenetically by infraorder from the most plesiomorphic (i.e., Enicocephalomorpha) to the most derived (i.e., the sister infraorders Cimicomorpha and Pentatomomorpha). Within each infraorder, superfamilies and families are alphabetical. Table 10.1 is arranged phylogenetically by infraorder and alphabetically by family, with the superfamily noted in parentheses for each.

OVERVIEW OF THE HETEROPTERA

The suborder Heteroptera has been separated into seven infraorders and at least 24 superfamilies (Schuh and Slater 1995, Henry 1997a). The following overview is based on currently accepted classifications of the Heteroptera by Štys and Kerzhner (1975), Schuh (1979), Štys (1985), Schuh (1986), Schuh and Štys (1991), W. Wheeler et al. (1993), Schuh and Slater (1995), Henry (1997a), and Polhemus and Polhemus (2008).

EUHETEROPTERA

Infraorder Enicocephalomorpha

Only two families are included in this infraorder. These unusual insects are often called unique-headed bugs because of the peculiar bilobed heads.

The Aenictopecheidae possess a protruding, often inflatable phallus and movable parameres, whereas in the Enicocephalidae (Fig. 10.1) the intromittent organ is reduced and noninflatable and the parameres are immobile, among other characters. These small, cryptic bugs range in size from 2 to more than 15 mm and are thought to prey on other arthropods. One African species of Enicocephalidae feeds on larvae of the ant *Rhoptromyrex transversiodis* Mayr (Bergroth 1915). Enicocephalids are well known for their swarming behavior, sometimes forming clouds of many thousands of individuals (Usinger 1945; Henry, personal observations in Pennsylvania, USA, and Mexico). About 10 genera and 20 species of Aenictopecheidae and 55 genera and 405 species of Enicocephalidae are known (Štys 1995a, 2002; Zoological Record 2003–2007). Wygodzinsky and Schmidt (1991) monographed the New World fauna, Štys (2002) provided a key to the enicocephalomorphan genera of the world, and Kerzhner (1995a) cataloged the Palearctic fauna.

Infraorder Dipsocoromorpha

This infraorder comprises only five families, all of which contain small, cryptically colored species, ranging in size from only 0.5 mm to about 4.0 mm. Most are found in rotting wood, water margins, or in the ground litter layer and similar conditions of tropical forest canopies. These tiny predatory insects are most abundant in the tropics. As Štys (1995b) noted for the Ceratocombidae, 'the number of undescribed species is enormous'.

Ceratocombids (Fig. 10.2) are characterized by long, slender antennae; two- or three-segmented tarsi on all legs; bristlelike setae on the antennae, head, and tibiae; and a short, distinct fracture at the middle of the costa on the hemelytra. Štys (1983) revised the group and provided keys to genera and higher groups. About eight genera and 51 species are known, most of which are tropical (Cassis and Gross 1995, Zoological Record 1996–2007). In the Nearctic only two genera and four species are known (Henry 1988b); in the

Palearctic only one genus and 11 species have been recorded (Kerzhner 1995b).

The Dipsocoridae (Fig. 10.3) usually possess three-segmented tarsi, long slender antennae with bristlelike setae, and a cuneus-like structure on the apical third of each hemelytron. They inhabit moist litter and rocky habitats along streams, ponds, lakes, and swampy areas, where they prey on coexisting arthropods. Emsley (1969) and Štys (1970) provided the most recent treatments. Two genera and 51 species are known (Cassis and Gross 1995, Zoological Record 1996–2007). Only one genus and two species occur in North America (Henry 1988c) and 2 genera and 12 species in the Palearctic Region (Kerzhner 1995b).

The Schizopteridae (Fig. 10.4) represent the largest family of Dipsocoromorpha with more than 42 genera and about 229 species (Cassis and Gross 1995, Zoological Record 1996–2007). Slater (1982) considered the world fauna largely undescribed and estimated that more than 1200 species exist. These bugs range in size from about 0.8 mm to nearly 2.0 mm and are characterized by their often convex, beetlelike forewings, subequally long first and second antennal segments, ventrally enlarged propleura, and hindlegs modified for jumping (Henry 1988h). Key works for this family are McAtee and Malloch's (1925) revision and Emsley's (1969) monograph, including a catalog of the world fauna.

The remaining dipsocoromorphan families are the Hypsipterygidae and Stemmocryptidae. The former contains only one genus of four species, one from Thailand and two from Africa (Štys 1995c, Redei 2007); the latter, based on a monotypic genus from New Guinea (Štys 1983), until recently, was the latest heteropteran family to be described.

NEOHETEROPTERA

Infraorder Gerromorpha

These are the aquatic true bugs, previously included in the Amphibicorisae (Dufour 1833, Leston et al. 1954). All are surface-inhabiting taxa found in a wide array of habitats from the smallest, often temporary, bodies of fresh water to the open oceans of the world. Eight families placed among four superfamilies are represented by more than 2000 species (Polhemus and Polhemus 2008).

Good general references on Gerromorpha include those by Brooks and Kelton (1967), Menke (1979), Andersen (1982), Schuh and Slater (1995), and Polhemus and Polhemus 2007, 2008), and catalogs by Henry and Froeschner (1988), Aukema and Rieger (1995), and Cassis and Gross (1995).

Gerroidea

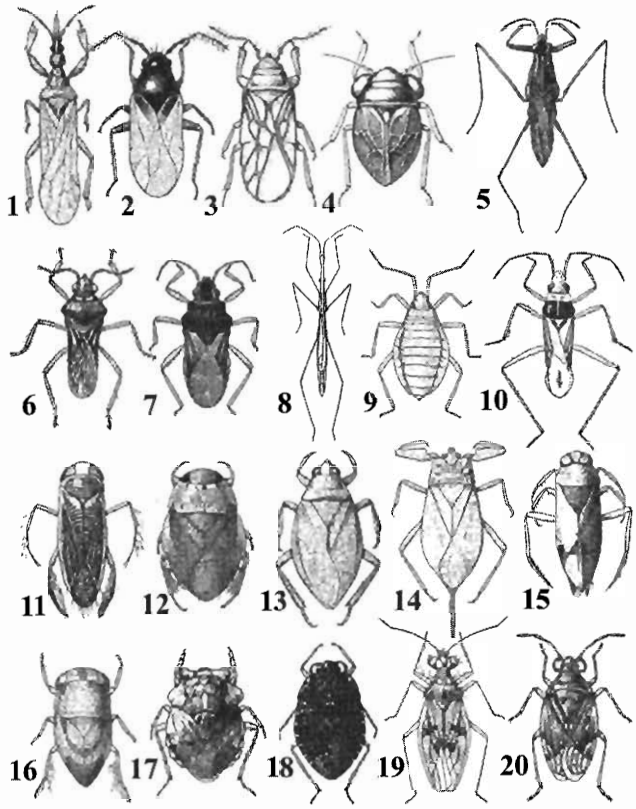
The Gerridae (Fig. 10.5), frequently called water striders or pond skaters, largely inhabit open water surfaces, including ponds, lakes, rivers, temporary pools, and even the open oceans (Smith 1988a). They are characterized by the elongate to globular, pile-covered bodies and long legs, usually with subapical claws. Wing dimorphism is common. Water striders range in size from about 1.6 mm to more than 36 mm for *Gigantometra gigas* (China) (Andersen 1982). About 67 genera and 751 species are known (Polhemus and Polhemus 2008).

The family Hermatobatidae, sometimes called seabugs, contains only one genus and nine species (Polhemus and Polhemus 2008). They are small elongate-oval marine bugs, ranging from 2.7 to 4 mm long, with relatively large eyes and strong claws for clinging to rocks. They are found along intertidal zones and are mostly predaceous (Cheng 1977).

The Veliidae (Fig. 10.6), commonly known as riffle bugs, small water striders, or broad-shouldered bugs, are characterized by the oval to more elongate body covered with water-repellent pile, relatively short legs, and multiple types of surface locomotion (Smith 1988c). They are found in both freshwater and saltwater habitats and may be found from mud flats and wet rocks to rapidly flowing streams and rivers (D. Polhemus 1997). Veliids represent the largest gerromorphan family, with 58 genera and 962 species (Polhemus and Polhemus 2008).

Hebroidea

The Hebridae (Fig. 10.7), or velvet water bugs, one of three families in the superfamily Hebroidea, are recognized by their apical claws, well-developed scutellum, and a rostral groove on the underside of the head. Hebrids are found in semiaquatic habitats along shorelines or on floating vegetation. They walk either on the water surface or along submerged plants protected



Figs. 10.1–10.20 Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, and Letopodomorpha. 10.1, Enicocephalomorpha: *Systelloderes biceps* (Say) [Enicocephalidae]. 10.2–10.4, Dipsocoromorpha: 10.2, *Ceratocombus vagans* McAtee and Malloch [Ceratocombidae]; 10.3, *Cryptostemma uhleri* McAtee and Malloch [Dipsocoridae]; 10.4, *Glyptocombus saltator* Heidemann [Schizopteridae]. 10.5–10.10, Gerromorpha: 10.5, *Gerris marginatus* Say [Gerridae: Gerroidea]; 10.6 *Microvelia ashlocki* Polhemus [Veliidae: Gerroidea]; 10.7, *Hebrus concinnus* Uhler [Hebridae: Hebroidea]; 10.8, *Hydrometra martini* Kirkaldy [Hydrometridae: Hydrometroidea]; 10.9, *Darwinivelia fosteri* Anderson and Polhemus [Mesoveliidae: Mesoveloidea]; 10.10, *Mesovelia mulsanti* White [Mesoveliidae: Mesoveloidea]. 10.11–10.15, Nepomorpha: 10.11, *Sigara hubbelli* (Hungerford) [Corixidae: Corixoidea]; 10.12, *Pelocoris carolinensis* Torre-Bueno [Naucoridae: Naucoroidea]; 10.13, *Belostoma flumineum* Say [Belostomatidae: Nepoidea]; 10.14, *Nepa apiculata* Uhler [Nepinae: Nepidae: Nepoidea]; 10.15, *Notonecta undulata* Say [Notonectidae: Notonectoidea]; 10.16, *Neoplea striola* (Fieber) [Pleidae: Notonectoidea]; 10.17, *Gelastocoris oculatus* (Fabricius) [Gelastocoridae: Ochteroidea]; 10.18, *Ochterus americanus* (Uhler) [Ochteridae: Ochteroidea]. 10.19, 10.20, Leptopodomorpha: 10.19, *Patapius spinosus* (Rossi) [Leptopodidae: Leptopodoidea]; 10.20, *Saldula galapagosana* Polhemus [Saldidae: Saldoidea]. (Figs. 10.1–10.3 after Froeschner 1944; 10.4, Henry 1988h; 10.5, 10.8, 10.11–10.18, Froeschner 1962; 10.6, 10.9, 10.20, Froeschner 1985; 10.7, 10.10, Froeschner 1949; 10.19, Froeschner and Peña 1985).

by their velvety hydrofuge pile (Polhemus and Polhemus 1988a). Nine genera and 221 species are known worldwide (Polhemus and Polhemus 2008).

Macroveliids are a small group of New World semi-aquatic bugs represented by only three genera and three species (Polhemus and Polhemus 2008). They are distinguished from true water striders by having apical claws. Found on surface vegetation, they prey or scavenge on other arthropods. The Paraphrynoveliidae are represented by only two southern African species, ranging in length from 1.7 to 2.4 mm (Andersen 1978, 1982). They resemble wingless hebrids and inhabit wet debris and water-soaked mosses along shorelines.

Hydrometroidea

The Hydrometridae (Fig. 10.8), often referred to as water treaders or water measurers, are the only family in the Hydrometroidea. These slender insects range in length from about 2.7 mm to nearly 22 mm and have long, slender legs and an elongate head. They are found primarily on emergent or floating vegetation, but some are found in more terrestrial habitats or on moist rock faces above streams or pools (Smith 1988b). About seven genera and 126 species are known worldwide (Polhemus and Polhemus 2008).

Mesovelioidae

Mesoveliids (Figs. 10.9, 10.10), often called pond treaders or pondweed bugs, are the sole representatives of the superfamily Mesoveloidea. These predatory bugs are small to medium sized, ranging from about 1.2 to 4.2 mm. They occur in diverse habitats, including open ponds and lakes to leaf litter on forest floors, water-soaked mosses, and seeping rock faces. Mesoveliidae are considered the sister group of all other Gerromorpha (Andersen 1982). Andersen and Polhemus (1980) provided a world checklist and Andersen (1982) gave a detailed morphological and phylogenetic review. Twelve genera and 46 species are known (Polhemus and Polhemus 2008).

PANHETEROPTERA

Infraorder Nepomorpha

The water bugs belonging to this infraorder include the taxa previously placed in the Hydrocorisae (Dufour 1933, Leston et al. 1954). They are characterized by short antennae that are concealed in part or entirely by the eyes. All are predatory, except for some Corixidae. Most can inflict painful bites. Except for the riparian Gelastocoridae and Ochteridae, all are aquatic and have legs modified for swimming (Schuh and Slater 1995).

Corixoidea

Corixids (Fig. 10.11), or water boatmen, ranging in length from 1.5 to 16 mm, are distinguished by their elongate-oval form, short unsegmented labium, one-segmented front tarsi, and short antennae. They swim dorsally using oarlike hind legs (Polhemus et al. 1988a). Most species inhabit fresh water but others have adapted to high concentrations of salt (Scudder 1976), where they forage for algae, protozoa, and metazoa, as well as other prey such as mosquito larvae and brine shrimp (Polhemus et al. 1988a). Thirty-five genera and 607 species are known (Polhemus and Polhemus 2008). Hungerford's (1948) revision of the New World fauna is the single most important reference of this family; Jansson (1986) treated the European corixids.

Naucoroidea

The Aphelocheiridae are a relatively small family of naucorid-like bugs, represented by only one genus containing approximately 78 species (Polhemus and Polhemus 2008). Members of this family represent one of the few insect groups that live their entire lives underwater, including mating, through the use of a plastron respiration system (Polhemus and Polhemus 1988a). The Potamocoridae, like the aphelocheirids, are a small group, previously considered a subfamily of the Naucoridae (Štys and Jansson 1988). Two genera and eight species are known. Aphelocheirids are found primarily in the Old World tropics, whereas potamocorids are known only from the Neotropics. The creeping water bugs, or Naucoridae (Fig. 10.12), represent the largest family of the Naucoroidea, with approximately 37 genera and 391 species found in all zoogeographic regions (Polhemus and Polhemus 2008). They are ovate, strongly dorsoventrally flattened, 5 to 20 mm long, and have raptorial forelegs for capturing prey. They occur in both flowing and still water where they live among submerged plants. Like many nepomorphans, these bugs can inflict a painful bite if carelessly handled (Polhemus and Polhemus 1988b).

Nepoidea

The Belostomatidae (Fig. 10.13), or giant water bugs, are the largest of the true bugs, ranging in length from 9 mm to more than 110 mm. Ovate and dorsoventrally flattened, they possess powerful raptorial forelegs, and breathe through straplike appendages at the tip of the abdomen. All are voracious predators that can attack

prey many times their size, subduing their victims with a powerful hydrolytic enzyme (J. Polhemus et al. 1988b). Eggs of most belostomatids are laid on emergent vegetation and other objects, but species of *Abedus* and *Belostoma* deposit their eggs on the backs of males (Smith 1976). The family classification was established by Laucke and Menke (1961). Nine genera and about 160 species are known (Polhemus and Polhemus 2008).

The Nepidae (Fig. 10.14), or waterscorpions, are a small group of dull brown, slender leaflike or sticklike insects, with raptorial forelegs and a long posterior respiratory siphon. Ranging in size from about 15 to 45 mm, nepids are found in fast- or slow-moving water, but prefer the latter where they wait submerged below the surface on floating plants and other debris for prey (D. Polhemus 1988). Fifteen genera and 268 species are known in the world (Polhemus and Polhemus 2008).

Notonectoidea

The Notonectidae (Fig. 10.15), or back swimmers, are a widespread group of elongate, medium-sized bugs ranging from 5 to 15 mm long. They are ventrally flattened and dorsally convex and have oarlike hind legs for swimming upside down. Backswimmers readily fly and often invade swimming pools where they can become a nuisance with the potential of inflicting painful bites to unwary swimmers (Polhemus and Polhemus 1988b). My only painful heteropteran bite – one that became extremely tender and throbbed for several days – came from naively holding a notonectid close-handed, while general collecting (about age 12) in submergent vegetation. Eleven genera and 400 species are known (Polhemus and Polhemus 2008).

The Pleidae (Fig. 10.16), or pygmy backswimmers, previously placed with the backswimmers until Esaki and China (1928) gave support for family status, are a small group of only three genera and 38 species. Like notonectids, these tiny predaceous insects range from 2 to 3 mm long and swim on their backs. They are strongly convex, possess coleopteriform or helmet-like hemelytra, and have slender hind legs, often set with long hairs (D. Polhemus 1988, Schuh and Slater 1995). The closely related Helotrephidae also were placed in the Notonectidae until given family rank by Esaki and China (1927), based on several unique characters, including the fused head and pronotum. About 21 genera and 180 species are known (Polhemus and Polhemus 2008).

Ochteroidea

Gelastocoridae (Fig. 10.17) are frequently called toad bugs because of their stout, oval bodies, usually roughened or warty upper surface, and ability to hop. They measure 6.0 to 10 mm long and occur along damp open areas near streams, ponds, lakes, and muddy ditches (Cassis and Gross 1995). Members of the genus *Nerthra* have been found in rotting logs and leaf litter far from water. The group occurs primarily in the Southern Hemisphere and is absent from most of the Palearctic. Todd (1955) revised the family. Three genera and 111 species are known (J. Polhemus 1995a, Polhemus and Polhemus 2008).

Ochteridae (Fig. 10.18), known as velvety shore bugs, are compact oval bugs, with nonraptorial forelegs and a velvety or soft-textured dorsum, often with scattered pale spots, frosted bluish areas, and golden setae (Polhemus and Polhemus 1988c, J. Polhemus 1995b). They live in damp areas along ponds, lakes, and streams where they feed on small arthropods. Three genera and 68 species are known (Polhemus and Polhemus 2008).

Infraorder Leptopodomorpha

This infraorder comprises four families separated into the superfamilies Leptopodoidea and Saldoidea, as defined by Schuh and Polhemus (1980).

Leptopodoidea

The Leptopodidae (Fig. 10.19) are generally elongate-oval, fast-moving predatory bugs measuring more than 2 mm long, usually with prominent or subpedunculate eyes. Many are found along streams and other wet areas, but some, such as the Palearctic *Patapius spinosus* (Rossi) introduced into Chile (Froeschner and Peña 1985) and USA (Sissom and Ray 2005), can be found far from water in semiarid conditions. Ten genera and 39 species are known (Polhemus and Polhemus 2008).

The Omaniidae have been called intertidal dwarf bugs. They are small, measuring only 1.15–1.59 mm

long, with large prominent eyes, coleopteriform hemelytra, and adhesive pads on the hind coxae. Only two genera and six species are known (Cobben 1970, Schuh and Slater 1995, Polhemus and Polhemus 2008).

Saldoidea

The family Aepophilidae is represented by only one genus and one species, *Aepophilus bonnairei* Signoret, often called the marine bug. These tiny predatory intertidal insects measure only about 2 mm, live among rocks, and survive below high tide with the aid of tiny hairs forming a plastron that traps a layer of air (Schuh and Slater 1995).

The Saldidae (Fig. 10.20), or shore bugs, represent the largest family of Lepopodomorpha with 29 genera and 335 species (Schuh et al. 1987, Polhemus and Polhemus 2008). They are fast-moving, medium-sized, oval to elongate bugs, with long antennae and four to five closed cells in the hemelytral membrane. These primarily predatory bugs are found mainly in littoral habitats along stream, lake, and marine shorelines, but can be found in numerous other situations, including wet vertical rock faces or in dry areas far from water (J. Polhemus 1988).

Infraorder Cimicomorpha

This infraorder is separated into seven superfamilies and 17 families, including the two largest heteropteran families, the Miridae and Reduviidae (Schuh and Štys 1991), and the most recently described heteropteran family, the Curaliidae (Schuh et al. 2008).

Cimicoidea

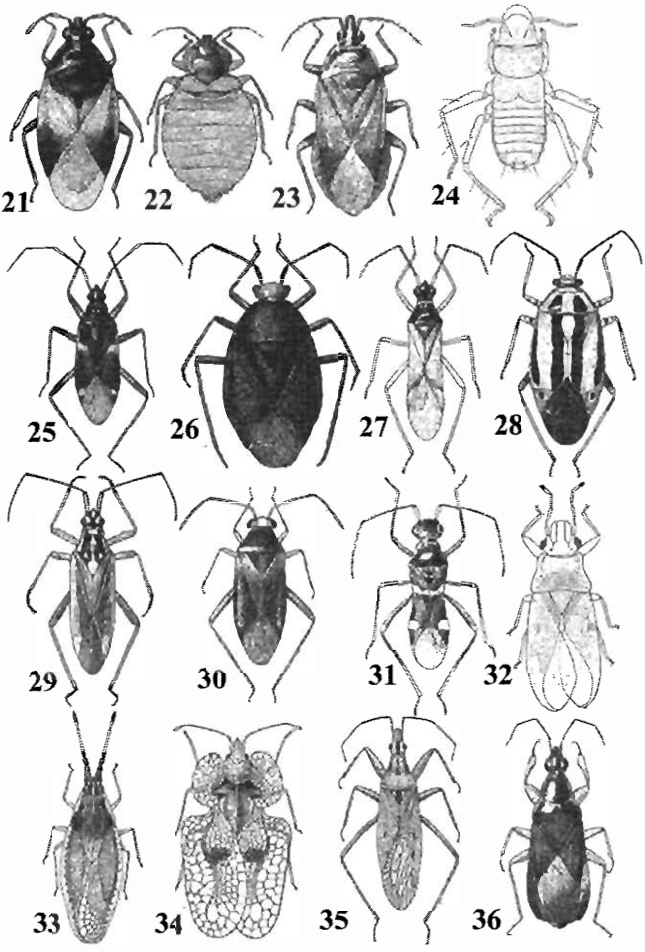
This superfamily contained only four families before Schuh and Štys (1991) proposed elevating the subfamilies of Anthocoridae to family status based on their hypothesis that shared traumatic insemination – where the male pierces the female body cavity during insemination – has evolved only once and, thus, supporting the monophyletic grouping with the 'nontraumatic' Lasiochilidae as sister to Anthocoridae, Cimicidae, Lyctocoridae, Plokiophilidae, and Polyctenidae. This classification has not gained general acceptance, however, and was not followed in the recent Australian (Cassis and Gross 1995) and Palearctic (Péricart 1996) catalogs. More recently, Tatarnic et al. (2006) presented another example of traumatic insemination in the Miridae. Herein, I follow Schuh and Štys (1991), with the realization that this classification is still in a state of flux. Eighty-two genera and 534 species of Anthocoridae (*sensu lato*) are known (Cassis and Gross 1995, Zoological Record 1996–2007).

Anthocoridae (Fig. 10.21), frequently called flower bugs or minute pirate bugs, are predatory, ranging in size from about 1.5 mm to 4.5 mm or more. Flower bugs are characterized by the fusiform antennal segments III and IV, the straight or forward-curving ostiolar canal, and the left paramere often grooved to accept the vesica. These bugs exhibit traumatic insemination (Péricart 1972, Schuh and Stys 1991). Many anthocorids are of great agricultural importance in biological control programs, especially the widely occurring genus *Orius* Wolff (Ryerson and Stone 1979, Lattin 1999, Hernández and Stonedahl 1999). Schuh and Slater (1995) provided a key to the tribes and Lattin (1999) reviewed the bionomics.

The Cimicidae (Fig. 10.22), often called bed bugs, are broadly oval, dorsoventrally flattened, wingless ectoparasites of birds and mammals. Cimicids range in size from about 4 mm to 12 mm. Of the 24 genera and 110 known species (Cassis and Gross 1995, Zoological Record 1996–2007), only two, the tropical bed bug *Cimex hemipterus* Fabricius and the human bed bug *C. lectularius* Linnaeus, are permanently associated with humans (Wheeler 1982). Most, however, are associated with birds and bats. All species exhibit traumatic insemination. Usinger (1966) monographed the family, and Ryckman et al. (1981) provided a world checklist and bibliography.

Lasiochilidae are a small family containing 10 genera and about 62 species, with most included in the genus *Lasiochilus*. They are about 3.0 to 4.0 mm long and are characterized by a posteriorly curved metathoracic scent-gland channel, a sickle-shaped left paramere, and nontraumatic insemination (Schuh and Slater 1995). These bugs are considered predators of various insect larvae under bark and in bracket fungi (Kelton 1978).

The family Lyctocoridae (Fig. 10.23) contains 27 species, all of which are placed in the genus *Lyctocoris*. Members of this predatory family resemble Anthocoridae and Lasiochidae, from which they were



Figs. 10.21–10.36 Cimicomorpha: 10.21, *Orius insidiosus* (Say) [Anthocoridae: Cimicoidea; 10.22, *Cimex lectularius* Linnaeus [Cimicidae: Cimicoidea]; 10.23, *Lyctocoris campestris* (Fabricius) [Lyctocoridae: Cimicoidea]; 10.24, *Hesperoctenes eumops* Ferris and Usinger [Polyctenidae: Cimicoidea]; 10.25, *Fulvius imbecilis* (Say) [Cylapinae: Miridae: Miroidea]; 10.26, *Bothynotus modestus* Wirtner [Deraeocorinae: Miridae: Miroidea]; 10.27, *Dicyphus agilis* (Uher) [Bryocorinae: Miridae: Miroidea]; 10.28, *Poecilocapsus lineatus* (Fabricius) [Mirinae: Miridae: Miroidea]; 10.29, *Leptopterna dolabrata* (Linnaeus) [Mirinae: Miridae: Miroidea]; 10.30, *Ceratocapsus modestus* (Uhler) [Orthotylinae: Miridae: Miroidea]; 10.31, *Cyrtopeltocoris illini* Knight [Phylinae: Miridae: Miroidea]; 10.32, *Xylastodorus luteolus* Barber [Thaumastocoridae: Miroidea]; 10.33, *Atheas mimeticus* Heidemann [Tingidae: Miroidea]; 10.34, *Corythuca ciliata* (Say) [Tingidae: Miroidea]; 10.35, *Nabis americoferus* Carayon [Nabidae: Naboidea]; 10.36, *Pagasa fusca* (Stein) [Nabidae: Naboidea]. (10.21–10.23, 10.25–10.31 after Froeschner 1949; 10.24, Froeschner 1988e; 10.32 redrawn after Barber 1920; 10.33–10.36, Froeschner 1944).

recently separated (Schuh and Štys 1991). A modified vesica, rather than the left paramere, is used during traumatic insemination (Schuh and Slater 1995). This primarily north temperate group of eight species includes one adventive species in the Nearctic (Henry 1988a) and 20, in the Palearctic (Péricart 1996).

The family Plokiophilidae, often called web lovers, includes small bugs about 1.2 to 3.0 mm long. They comprise about 13 species separated into five genera (Štys 1991, Carpintero and Dellapé 2005, Schuh 2006) placed in two subfamilies. Mating involves traumatic insemination. The Embiophilinae, containing only one genus and three species, are associated with the Embioptera, whereas all Plokiophilinae are associated with spiders, where they feed on insects entrapped in their host's webs (Eberhard et al. 1993).

The Polyctenidae (Fig. 10.24), or the bat bugs, are a small group of wingless, viviparous ectoparasites comprising five genera and 32 species. Bat bugs range in size from 3 to 5 mm and are dorsoventrally flattened, lack compound eyes and ocelli, possess setal combs or ctenidia, and have traumatic insemination (Slater 1982, Cassis and Gross 1995, Schuh and Slater 1995). Polyctenids never leave their bat hosts and transfer to other individuals only by direct contact (Marshall 1982). Ferris and Usinger (1939), Maa (1964), and Ueshima (1972) provided key revisions of the family and Ryckman and Sjogren (1980) cataloged the world fauna.

Joppeicoidea

Only one family is included in this superfamily. The family Joppeicidae is represented by one species, *Joppeicus paradoxus* Puton, found only in Israel, Egypt, and Sudan. These tiny anthocorid-like bugs, about 3.0 mm long, possess several unique wing, abdominal, and genital characters that make it difficult to place them phylogenetically (Davis and Usinger 1970). They have been found under stones and other objects, in caves, under bark, and with bat bugs (Cimicoidea: Polyctenidae) (Štys 1971).

Microphysoidea

The Microphysidae are a small group of predatory bugs, only about 1.5 to 3.0 mm long, that resemble certain species of Anthocoridae. Five genera and 25 species are known (Schuh and Slater 1995, Zoological Record 1996–2007). The Palearctic species are all strongly sexually dimorphic, with the females usually brachypterous, whereas the only two endemic Nearctic species, *Chinaola quercicola* Blatchley and *Mallochiola gagates* (McAtee and Malloch), are similar in both sexes. Microphysids are often found on the bark of trees (Péricart 1972) or are associated with lichens and mosses growing on the trunks and larger branches of trees and shrubs (Henry 1988e). *Chinaola quercicola* is associated with foliose lichens growing on *Juniperus virginiana* (Cupressaeae) in South Carolina and Virginia (Wheeler 1992).

Miroidea

The Miroidea contains three families: Miridae, Thaumastocoridae, and Tingidae. The Thaumastocoridae were first placed in the Cimicomorpha by Drake and Slater (1957) and later were considered the sister group of the Tingidae by Schuh and Štys (1991), who included both in the Mirioidea with the Miridae.

The Miridae, or plant bugs, represent the largest family in the Heteroptera, with more than 1300 genera and 10,040 species, or about 25% of the true bugs. They are currently separated into eight subfamilies (Schuh 1995, Cassis and Gross 1995, Cassis et al. 2006). Since the appearance of the Carvalho catalog (1957–1960), considerable attention has been given to the family. Henry and Wheeler's (1988) catalog of the North American fauna and Cassis and Gross's (1995) catalog of the Australian fauna were followed by Schuh's (1995) world catalog, now available online at http://research.amnh.org/pbi/catalog/. More recently, Kerzhner and Josifov (1999) cataloged the Palearctic fauna with great detail devoted to distribution and key literature.

Carvalho's (1955) now largely outdated keys to subfamilies, tribes, and genera are a remarkable attempt to identify the Miridae on a world basis. Since then, changes in the classification and the emergence of numerous workers have made it difficult to update these keys on such a large scale. Schuh and Slater (1995) provided the most recent key to subfamilies, largely following the classification supported by Schuh (1974, 1976). The most recent works on a regional basis are found in the catalogs cited above.

Mirids range in size from about 1.5 mm in certain species of Bryocorinae, Orthotylinae, and Phylinae, especially brachypterous forms, to 15 mm or more in some of the Neotropical species of Resthenini (Mirinae). Many plant bugs are brightly colored red, orange, and yellow, often with spots and stripes, whereas the majority are less spectacular gray, brown, or black, blending in remarkably well with their surroundings (Henry and Wheeler 1988, Wheeler and Henry 2004). Numerous species, such as the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), and lygus bugs, *Lygus* spp., in North America, cocoa capsids, *Distantiella theobroma* (Distant) and *Sahlbergella singularis* Haglund, in Africa, and tea bugs, *Helopeltis* spp., in Asia and India, are major agricultural pests (Wheeler 2000a, 2001), whereas many others are predatory and often beneficial in agroecosystems (Wheeler 2000b, 2001).

The habits and biology of the Miridae have been documented in numerous, widely scattered publications. Certain classical treatments, such as those by Kullenberg (1944), Southwood and Leston (1959), Putshkov (1966), and Ehanno (1983–1987), represent important sources of biological information. These and numerous other references have been examined by Wheeler (2001), who synthesized data on biology, hosts, and habits, bringing the knowledge of the family to a new level. The subfamily Isometopinae, often called jumping tree bugs, contains mostly small bugs about 2 to 3 mm, but one giant from Sumatra, *Gigantometopus rossi* Schwartz and Schuh (1990), which is nearly 7.0 mm. About 175 species are known (Herczek 1993, Schuh 1995, Akingbohungbe 1996). They are characterized by their often holoptic eyes, unusually shaped, often

anteriorly flattened head, saltatorial hind legs, and the possession of ocelli, a character unique and considered plesiomorphic in the Miridae. Isometopines, once thought to be associated with mosses and lichens, are now known to be specialized predators of scale insects (Hemiptera: Coccoidea) (Wheeler and Henry 1978). Henry (1980) gave a key to the New World genera and Ghauri and Ghauri (1983), a key to world genera. More recently, Herczek (1993) analyzed relationships and Akingbohungbe (1996) revised the African, European, and Middle Eastern faunas.

The Cylapinae (Fig. 10.25) are a small subfamily of primarily tropical bugs characterized by long, slender, apically toothed claws and an unusually long labium extending well onto the abdomen. This subfamily is separated into three tribes (Carvalho 1957, Kerzhner and Josifov 1999), though the Bothriomirini and Fuliviini have been treated as synonyms of Cylapini (Schuh 1995). The New World genus *Cylapus*, quick-moving bugs with unusual stalked eyes, are often associated with fungi on rotting logs and have been long thought to be predatory. Wheeler and Wheeler (1994), however, observed that the gut contents of *Cylapus tenuis* Say from New York and *Cylapus* sp. from Peru contained pyrenomycete spores, seemingly demonstrating that at least some members of this genus are mycophagous. Members of the fulviine genus *Fulvius* Stål, on the other hand, are often found under loose bark and are probably predators of coexisting arthropods (e.g., Kelton 1985, Wheeler 2001). The recently described *Rhyparochromomiris femoratus* Henry and Paula, remarkable in being the only mirid with swollen rhyparochromid-like forefemora, strongly resembles certain myrmecomorphic herdoniine Mirinae (Henry and Paula 2004).

The subfamily Deraeocorinae (Fig. 10.26), the fifth largest subfamily with more than 100 genera separated into six tribes, is recognized by the distinct pronotal collar, usually punctate dorsum, and claws with setiform parempodia and cleft or toothed bases (Schuh and Slater 1995). Members of the genus *Deraeocoris* Kirschbaum are well known for their predatory habits and may be useful in biological control programs. For example, Wheeler et al. (1975) showed that *D. nebulosus* (Uhler) in North America is an effective predator of numerous ornamental pests, including lace bugs, white flies, and mites. The Termatophylini, recently revised by Cassis (1995), are unusual in resembling certain species of Anthocoridae. Most members of the tribe are specialized thrips predators, although a few have been associated with lepidopteran larvae (Cassis 1995). Wheeler (2001) documented the feeding behavior of three New World thrips specialists in the genus *Termatophylidea*. Ferreira (2000, 2001) revised and provided a key to the 17 genera of the New World tribe Clivinematini, many of which prey on ensign scales (Ortheziidae) (Wheeler 2001). Members of the Old World hyaliodine genus *Stethoconus* are tingid specialists, including *S. japonicus* Schumacher, recently reported in North America, which feeds on the azalea lace bug *Stephanitis pyrioides* (Scott) (Henry et al. 1986).

The Bryocorinae (Fig. 10.27), representing the fourth largest subfamily, are a mixed group comprising three tribes, with about 200 genera (Schuh and Slater 1995). The tribe Bryocorini contains only five genera, all of which are restricted to ferns. The largest and most widespread genus, *Monalocoris*, contains 15 species and occurs in all zoogeographic regions. The tribe Eccritotarsini is largely a New World group recognized by large, disc-shaped pulvilli; the largest genus, *Eccritotarsus*, which undoubtedly is not monophyletic, contains about 90 species, most of which are distinguished by the male genitalia and distinct dorsal color pattern of many species (Carvalho and Schaffner 1986, 1987). Eccritotarsines produce characteristic chlorosis or leaf spotting on their hosts, making many of them potentially serious ornamental and crop pests. In the USA, *Halticotoma valida* Townsend severely discolors the foliage of certain species of ornamental *Yucca* spp., often killing entire plants (Wheeler 1976a). Members of the genus *Tenthecoris* are well-known pests of orchids (Hsaio and Sailer 1947), and *Pycnoderes quadrimaculatus* (Guérin-Méneville) causes serious injury to beans and other garden crops (Wehrle 1935, Wheeler 2001). Within the Dicyphini, subtribe Odoniellina, *Distantiella theobroma* (Distant) and *Sahlbergella singularis* Haglund are among the most devastating cocoa pests (Entwistle 1972, Wheeler 2001), whereas in the subtribe Dicyphina, *Macrolophus melanotoma* (Costa) is being used effectively to control whiteflies in European greenhouses (Schelt et al. 1996, Wheeler 2001). Many members of this subtribe live on glandular-hairy plants where they prey on insects entrapped on the viscid surfaces of stems, leaves, and flower clusters (Henry 2000d, Wheeler 2001).

The Mirinae (Figs. 10.28, 10.29) represent the largest subfamily, comprising more than 300 genera and six tribes. Members of this group are characterized by the distinct pronotal collar and widely divergent,

fleshy pretarsal parempodia. The tribe Herdoniini contains some of the most remarkable ant mimics in the Heteroptera. The North American *Barberiella formicoides* Poppius is so closely tied to its associated ant species that the brown early instars resemble the smaller, brown *Lasius neoniger* Emory (Formicidae) and the black later instars resemble the larger, black *Camponotus nearcticus* Emery and *Formica subsericea* Say (Formicidae) (Wheeler and Henry 1980). The largest Miridae are found in the aposomatically colored tribe Restheniini. *Callichilella grandis* (Blanchard) and *Resthenia scutata* Spinola rival each other for the title of the world's largest mirid, each measuring 15 mm or more. Members of the Old World tribe Mecistoscelini are mostly bamboo specialists (Wheeler 2001), and the much larger, worldwide tribe Stenodemini also are grass specialists, with many species, such as *Leptopterna dolabrata* (Linnaeus) (Wheeler 2001), *Notostira elongata* (Geoffroy) (Bockwinkel 1990), and *Trigonotylus caelestialium* (Kirkaldy) (Wheeler and Henry 1985), causing economic injury to pasture grasses, forage crops, and small grains (Henry and Wheeler 2007). The clear-winged Hyalopeplini, containing about 15 genera, are restricted to the Old World, with the exception of *Hyalopeplus pellucidus* (Stål) also found in Hawaii (Carvalho 1979). The nominate tribe Mirini, by far the largest tribe, contains some of the most important crop pests (Wheeler 2000a, 2001), including the infamous lygus bugs, *Lygus* spp. (Schwartz and Foottit 1998). This tribe also can claim the largest heteropteran genus, the largely predatory *Phytocoris*, with more than 500 described species (Stonedahl 1988).

The Orthotylinae (Fig. 10.30) are a large, diverse group recognized by the convergent pretarsal parempodia and the often large and complex male genitalia. This subfamily contains more than 220 genera and is separated into three to five tribes (Schuh 1995, Henry 2000c), but this level of classification needs considerable revision, especially the nominate tribe Orthotylini that certainly is at least paraphyletic. A large number of remarkable ant-mimetic or myrmecomorphic taxa occur in this group, especially in ceratocapsine genera such as *Ceratocapsus, Pilophoropsis*, and *Schaffneria* (Wheeler 1991, Henry 1994), and the halticine *Myrmecophyes oregonensis* Schuh and Lattin (1980). Also, included here are a number of pest species that cause heavy foliar chlorosis, such as the garden fleahopper, *Halticus bractatus* (Say), the phlox plant bug, *Lopidea davisi* Knight, and a broom plant bug, *Melanotrichus virescens* (Douglas and Scott) (Wheeler 2001). Numerous others, such as the black-kneed capsid, *Blepharidopterus angulatus* (Fallén), *Heterotoma planicorne* (Pallas), and species of *Hyalochloria* (Wheeler and Henry 1992, Henry 2001), are important predators of aphids, whiteflies, lepidopteran larvae, and other arthropods, including mites. In a recent study of the Old World genus *Coridromius*, Tatarnic et al. (2006) described the third independent case of traumatic insemination in the Heteroptera.

The second largest subfamily, the Phylinae (Fig. 10.31), with about 300 genera separated into five tribes, is characterized by hairlike parempodia and a straplike vesica (Schuh and Slater 1995). Comprehensive revisions of the South African (Schuh 1974) and the Indo-Pacific Regions (Schuh 1984) are good sources of information on this highly variable group. Most phylines are oval or elongate-oval, but many are myrmecomorphic, such as the Asian *Biliranoides* (Schuh 1984), *Coquillettia* (McIver and Stonedahl 1987), and *Pilophorus* (Schuh and Schwartz 1988), as well as most members of the tribe Hallodapini (Schuh 1974). *Campylomma verbasci* (Meyer-Dür), a widely studied species that can be a pest in fruit orchards, is more often considered a useful predator preying on mites, aphids, and leafhoppers (Braimah et al.1982, Wheeler 2001). The attractive, mostly red, azalea plant bug, *Rhinocapsus vandueei* Uhler, from the eastern USA frequently bites gardeners, causing red, swollen welts similar to mosquito bites (Wheeler and Herring 1979). Species of *Ranzovius* are obligate spider web commensals, scavenging on entrapped insects and possibly preying on spider eggs and molting spiderlings (Wheeler and McCaffrey 1984, Henry 1999).

Thaumastocorids (Fig. 10.32) are a small group of bugs with only 18 species in six genera, ranging from about 2.0 mm to nearly 5.0 mm (Cassis and Gross 1995, Schuh and Slater 1995, Carpintero and Dellapé 2006). The royal palm bug, *Xylastodoris luteolus* Barber, is a serious pest of royal palm (*Roystonea* spp.: Arecaceae) in Cuba and South Florida (Baranowski 1958). Members of the subfamily Thaumastocorinae are Old World, with most found in Australia, but one new species, recently described from Argentina causing serious damage to ornamental *Eucalyptus* spp. in LaPlata, is considered an immigrant from Australia (Carpintero and Dellapé 2006). Drake and Slater (1957) studied the classification of the family, which has no common name, though members of the New World subfamily

Xylastodorinae are often called palm bugs because of their general host association.

The Tingidae are a relatively large group of often ornate, lacy, phytophagous bugs separated into three subfamilies, with about 260 genera and 2124 species. They range in size from 2.0 mm to more than 8.0 mm (Drake and Ruhoff 1965, Cassis and Gross 1995, Schuh and Slater 1995, Zoological Record 1996–2007).

The Cantacaderinae are a small group of elongate-oval species with mostly opaque, rather than lacy, hemelytra, found primarily in the Southern Hemisphere. Thirty-five genera and 135 species are known (Froeschner 1996). Most workers have considered Catacaderinae a subfamily of the Tingidae, but B. Lis (1999) argued to give it family status. Schuh et al. (2006), however, presented convincing evidence for retaining them as a tingid subfamily. Froeschner (1996) provided keys to the two tribes, Cantacaderini and Phatnomatini, and their respective genera.

The Vianaidinae are restricted to the Neotropics and contain only two genera and five species (Drake and Ruhoff 1965). Although most known specimens lack eyes and are flightless, with beetlelike hemelytra, a few macropters with well-developed compound eyes have been collected (Schuh et al. 2006). Kormilev (1955) accorded family status to the group, but most recent authors have given the vianaidines subfamily status within the Tingidae (Schuh and Stys 1991, Schuh et al. 2006).

The Tinginae (Figs. 10.33, 10.34) is by far the largest subfamily, with all of the remaining 230 genera and majority of species found here. Most of the taxa included in this subfamily are the typically lacy species from which the common name 'lace bug' is derived. The classification, with only four tribes, needs attention, particularly the Tingini (Drake and Ruhoff 1965, B. Lis 1999, Schuh et al. 2006). This group contains the most important crop and ornamental pests in the family, such as the cotton lace bug, *Corythucha gossypii* (Fabricius), a widespread New World tropical and subtropical pest of herbs, shrubs, and trees that was recently discovered in Hawaii (Miller and Nagamine 2005) and American Samoa (Henry, personal observation) where it threatens to become a pest of truck crops. Another example is the North American sycamore lace bug, *Corythucha ciliata* (Say), which has become established in the Old World where it quickly has become a pest of *Platanus* spp. in much of Europe east to Japan and Korea (Heiss 1995, Tokihiro et al. 2003). In contrast, the New World lantana lace bug, *Teleonemia scrupulosa* Stål, has been introduced into Australia, Asia, and Africa as a biological control agent of the invasive weed *Lantana camara* (Verbenaceae) (Harley and Kassulke 1971). Maternal care is well known for some members of the genus *Gargaphia* (Tallamy and Schaefer 1997).

Naboidea

The family Medocostidae contains only one African genus and one species, *Medocostes lestoni* Štys (Štys 1967a, Kerzhner 1989). This bug is unique in having the fourth segment of the labium subequal to the lengths of segments two and three combined. Its habits are little known, but it is thought to prey on bark-inhabiting insects (Kerzhner 1989).

The Nabidae (Figs. 10.35, 10.36), or damsel bugs, represent a relatively small group of important generalist predators. Thirty-one genera and 386 species are known (Lattin 1989, Cassis and Gross 1995, Zoological Record 1996–2007). Previously, four subfamilies were included, but the Medocostinae and Velocipedinae were removed and given family rank by Schuh and Štys (1991), leaving only the Nabinae and Prostemmatinae. Prostemmatines are largely ground-dwelling predators, whereas the nabines are more frequently found on plants and are often used in biological control of crop pests (Lattin 1989). Members of the New World genus *Arachnocoris*, the only genus included in the tribe Arachnocorini (Nabinae), are obligate spider commensals that have modified claws for traversing spider webs (Myers 1925; Henry 1984, 1999). The most important taxonomic works on the Nabidae are those by Harris (1928) for the North American species, Kerzhner (1981) for the fauna of the former USSR, and Péricart (1987) for the western European species.

Reduvioidea

The Reduvioidea comprise only two families, the Pachynomidae and Reduviidae. Although the Pachynomidae were long considered related to the Nabidae (e.g., Cobben 1968, 1978), they are now considered to be the sister group of the Reduviidae (Weirauch 2008). Pachynomids range in length from 3.5 to 15 mm and resemble prostemmatine nabids. Only four genera and 15 species in two

subfamilies of this primarily tropical group are known (Carayon and Villiers 1968).

The Reduviidae (Figs. 10.37–10.41), or assassin bugs, represent the second largest heteropteran family. About 981 genera and more than 6878 species (Froeschner and Kormilev 1989, Maldonado 1990, Cassis and Gross 1995, Putshkov and Putshkov 1996, Zoological Record 1996–2007) are known, with most occurring in the tropics. These predatory bugs range in size from a few millimeters to more than 40 mm for species of the New World harpactorine genus *Arilus* or the heavy-bodied African species of the ectrichodiine genus *Centraspis*. Most reduviids can inflict painful bites if handled carelessly, with the exception of the Triatominae that are capable of painlessly taking blood meals from their vertebrate hosts, including humans, because of the anesthetizing action of the bug's saliva (Lent and Wygodzinsky 1979). The suprageneric classification has been in serious need of study. Putshkov and Putshkov (1985–1989) listed 21 subfamilies, Maldonado (1990) recognized 25, Cassis and Gross (1995) documented 26, and, most recently, Putshkov and Putshkov (1996) listed 23. The Phymatinae, long treated as a separate family (Froeschner and Kormilev 1989, Maldonado 1990), are now considered a subfamily within the Reduviidae (Cassis and Gross 1995, Schuh and Slater 1995, Putshkov and Putshkov 1996). More recently, Weirauch (2008) gave strong support for 21 subfamilies based on the first cladistic analysis of the family using 162 morphological characters.

Of the major subfamilies, the Ectrichodiinae contains some of the largest species. They are usually stout bodied, bright red and black, and sexually dimorphic with females often brachypterous. Approximately 300 species occur circumtropically. All are thought to be obligate milliped predators (Louis 1974). Cook (1977) treated the Asian species and Dougherty (1980), the Neotropical ones.

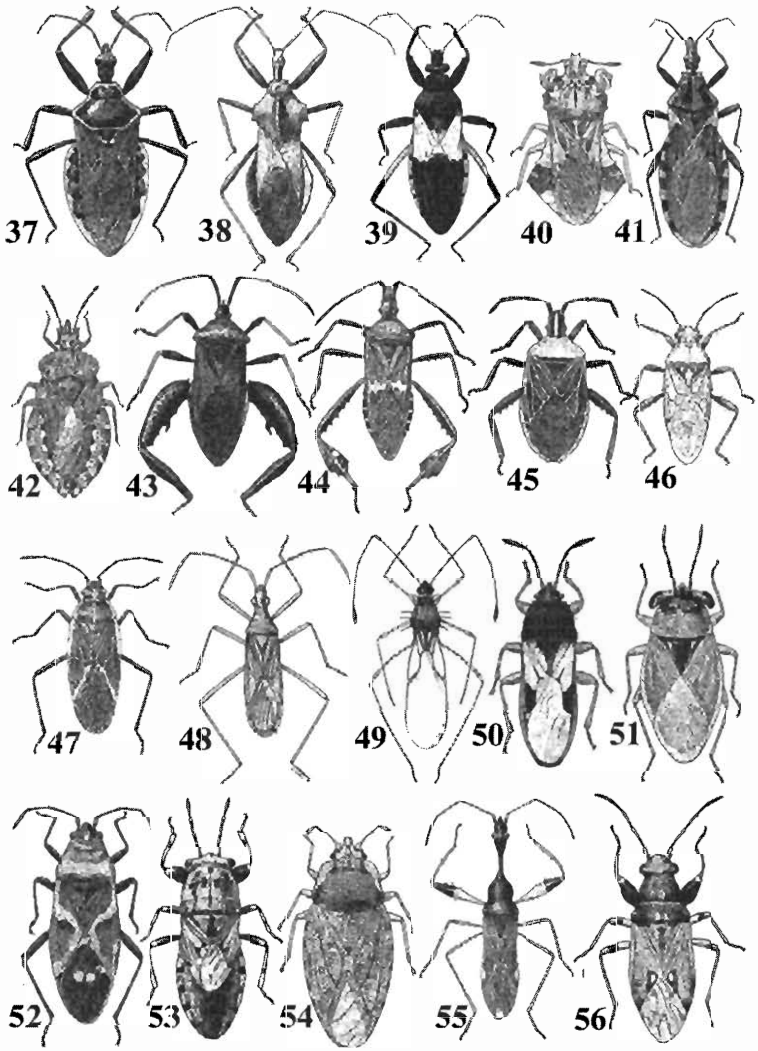
The Emesinae, or thread-legged bugs, are generally delicate, slender bugs, with long, thread-thin legs. They range from about 3 mm in some species of *Empicoris* to some of the quite long species of *Berlandiana* and *Emesaya*, measuring more than 36 mm. Emesines are mostly nocturnal predators, with some known to live in spider webs (e.g., Hickman 1969), whereas several others feed on mosquitoes and sand flies (Hribar and Henry 2007). Wygodzinsky's (1966) profusely illustrated monograph is the most important source of information on emesine biology and systematics.

The Harpactorinae (Figs. 10.37, 10.38) represent the largest and one of the most diverse reduviid subfamilies with more than 288 genera and more than 2000 species worldwide. They range from the stout, oval-bodied Apiomerini, with modified forelegs, to the large wheel bug, *Arilus cristatus* (Say), named for the large crest-shaped wheel on the pronotum. Certain genera, such as the genus *Graptocleptes*, form a mimicry complex with certain species of wasps. Harpactorines are general predators with many specializing on insect larvae. Barber (1920) and Moul (1945) documented more than 25 different prey for the wheel bug; preserved prey in the USNM collection include a grasshopper, *Melanoplus* sp. (Orthoptera: Acrididae); the Carolina mantid, *Stagmomantis carolina* (Johannson) (Mantodea: Mantidae); a walkingstick, *Diapheromera femorata* (Say) (Phasmatodea: Heteronemiidae); a paper wasp, *Polistes* sp. (Hymenoptera: Vespidae); and honeybees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae).

The Phymatinae (Fig. 10.40), or ambush bugs, until relatively recently were given their own family status, but recent acceptance of evidence for subfamily status within the Reduviidae (Carayon et al. 1958) is now followed by most workers (e.g., Putshkov and Putshkov 1996). Ambush bugs are stout bodied, often tuberculate, and well-camouflaged diurnal predators, frequently lying in wait within flowers or flower clusters to grab prey with their strongly modified, raptorial forelegs. About 26 genera and 281 species are known (Froeschner and Kormilev 1989). The most recent taxonomic treatments are by Kormilev (1962) and Maa and Lin (1956); Froeschner and Kormilev (1989) cataloged the world fauna and gave keys to species for all genera, except *Lophoscutus* and *Phymata*.

The Reduviinae, with about 138 genera and nearly 1000 species, are a cosmopolitan group recognized in part by the presence of ocelli and the absence of a discal cell on hemelytra (Maldonado 1990, Cassis and Gross 1995). Weirauch (2008) has shown that this subfamily is polyphyletic, indicating significant changes will be forthcoming. Most of the taxa now included in the subfamily are generalist predators, but certain species are associated with stored products or humans, such as the masked hunter, *Reduvius personatus* (Linnaeus), that occasionally bites people and has acquired the popular name 'kissing bug'.

The Salyavatinae are a small subfamily of medium-sized, mostly Old World assassin bugs, with only 15 genera and 99 species (Maldonado 1990). Little



Figs. 10.37–10.56 Cimicomorpha and Pentatomomorpha. 10.37–10.41. Cimicomorpha. 10.37, *Apiomerus crassipes* (Fabricius) [Harpactorinae: Reduviidae: Reduvioidea]; 10.38, *Arilus cristatus* (Say) [Harpactorinae: Reduviidae: Reduvioidea]; 10.39, *Microtomus purcis* (Drury) [Micotominae: Reduviidae: Reduvioidea]; 10.40, *Phymata pennsylvanica* Handlirsch [Phymatinae: Reduviidae: Reduvioidea]; 10.41, *Triatoma sanguisuga* (Leconte) [Triatominae: Reduviidae: Reduvioidea]. 10.42–10.56, Pentatomomorpha. 10.42, *Aradus acutus* Say [Aradidae: Aradoidea]; 10.43, *Acanthocephala femorata* (Fabricius) [Coreinae: Coreidae: Coreoidea]; 10.44, *Leptoglossus phyllopus* (Linnaeus) [Coreinae: Coreidae: Coreoidea]; 10.45, *Chelinidea vittiger* Uhler [Coreinae: Coreidae: Coreoidea]; 10.46, *Arhyssus lateralis* (Say) [Rhopalinae: Rhopalidae: Coreoidea]; 10.47, *Boisea trivittata* (Say) [Serinethinae: Rhopalidae: Coreoidea]; 10.48, *Dicranocephalus insularis* (Dallas) [Stenocephalidae: Coreoidea]; 10.49, *Pronotacantha annulata* Uhler [Berytidae: Lygaeoidea]; 10.50, *Blissus leucopterus* (Say) [Blissidae: Lygaeoidea]; 10.51, *Geocoris punctipes* (Say) [Geocoridae: Lygaeoidea]; 10.52, *Lygaeus kalmii* Stål [Lygaeidae: Lygaeoidea]; 10.53, *Phlegyas abbreviatus* (Uhler) [Pachygronthidae: Lygaeoidea]; 10.54, *Parapiesma cinereum* (Say) [Piesmatidae: Lygaeoidea]; 10.55, *Myodocha serripes* Olivier [Myodochinae: Rhyparochromidae: Lygaeoidea]; 10.56, *Pseudopachybrachius basalis* (Dallas) [Myodochinae: Rhyparochromidae: Lygaeoidea]. (10.37–10.41 after Froeschner 1944; 10.42–10.47, 10.50–10.56, Froeschner 1942; 48, Froeschner 1985; 10.49, Froeschner and Henry 1988.)

information is available on these unusual, often spined bugs, except for the New World *Salyavata variegata* Amyot and Serville, popularly known as the 'fishing bug' (McMahon 2005) because of the way it captures its primary prey, species of *Nasutitermes* termites. The well-camouflaged immatures use previously fed-upon termite carcasses to bait and capture new termite prey from their nests (McMahon 1983).

The Stenopodainae are mostly tropical bugs with about 114 genera and more than 720 species (Maldonado 1990). They are dull colored, with a large closed cell on the hemelytra. Most apparently they are ground dwelling and not often collected, except in Malaise traps or at lights (personal observations).

The Triatominae (Fig. 10.41), or conenoses, though not a large group (about 116 species), are of great medical importance because they are vectors of the trypanosome, *Trypanosoma cruzi*, the causal agent of Chagas' disease (American trypanosomiasis), an often fatal disease of humans in the Neotropics. Another triatomine, *Rhodnius prolixus* Stål, is a well-known test animal in insect physiology studies (Wigglesworth 1972). Lent and Wygodzinsky (1979) monographed the subfamily and gave detailed information about Chagas' disease vectors.

Velocipedoidea

Two families are currently placed in the Velocipedoidea, the Curaliidae and the Velocipedidae. The Curaliidae, represented by only one genus and one species, is the most recently recognized family within the Heteroptera (Schuh et al. 2008). *Curalium cronini* Schuh, Weirauch, and Henry, measuring only 1.75 mm long, is characterized by four or five closed cells on the wing membrane, placing it as the sister group of the Velocipedidae, the only other cimicomorphan family with such cells. This tiny, deep red, anthocorid like, probable predator, coined the 'ruby bug' for its bright color, is known only from lights in Florida and Louisiana.

Velocipedidae are a small, poorly known group of somewhat broadly oval species, measuring about 10 to 15 mm long. Nothing is known of their feeding habits, but their mouthparts are similar to those found in some aquatic families (Kerzhner 1981), suggesting that they are predatory. Four genera and 25 species are known from northeastern India to New Guinea (Schuh and Slater 1995, Doesberg 2004).

Infraorder Pentatomomorpha

Henry (1997a), in a phylogenetic analysis of the Pentatomomorpha, recognized six superfamilies. The monophyly of the Pentatomomorpha, including Aradoidea, is supported by at least six synapomorphies that include the presence of lamellate pulvilli, abdominal trichobothria (lost in the Aradoidea), an apically bulbous spermatheca, similar accessory salivary glands, an embryonic egg burster, and lack of a true operculum. Based on studies of the pregenital abdomen and lack of abdominal trichobothria, however, Sweet (1996) gave the Aradoidea infraorder status. Nevertheless, Schuh (1996) and Henry (1997a) did not follow Sweet's proposal based on the strong character support for placement of the Aradoidea in the Pentatomomorpha. Cassis and Gross (2002) followed the latter conclusion, stating an alternative hypothesis is not well supported. Henry (1997a) provided a key to the pentatomomorphan superfamilies and families composing the newly revised Lygaeoidea.

Aradoidea

The Aradidae (Fig. 10.42), frequently called flat bugs, are generally dull brown to black, strongly dorsoventrally flattened, oblong-oval bugs, measuring from 3 mm to more than 11 mm (Schuh and Slater 1995). Most have a strongly granulate body surface, often with tubercles and deep ridges or punctures, making them remarkably cryptic on and under bark of living and dead trees. Many are wingless or brachypterous. Aradids have unusually long maxillary stylets that coil within the head and possess typical pentatomomorphan characteristics, except for the absence of abdominal trichobothria, which are hypothesized as a character loss (Henry 1997a). Most species have been associated with various kinds of fungi (Usinger 1936, Kormilev and Froeschner 1987, Froeschner 1988a). *Aradus cimamomeus* Panzer, however, feeds on living tissue, causing serious injury to species of *Larix* and *Pinus* (Pinaceae) in Europe (Strawinsky 1925, Helioevaara 1984). About 233 genera and 1931 species of Aradidae are separated into eight subfamilies (Kormilev and Froeschner 1987, Cassis and Gross 2002, Zoological Record 2003–2007).

The family Termitaphidae comprises small, 2–3 mm, scalelike bugs that, like the Aradidae, have long stylets held coiled inside the head cavity. All species are

known only from termite nests. Two genera and nine species are known, with most occurring in the Neotropics (Usinger 1942). Myers (1924) and Usinger (1942) reviewed and provided keys to the world fauna, and Myers (1932) and Usinger (1942) gave notes on the biology and habits of several species.

Coreoidea

Schaefer (1965) included the families Alydidae, Coreidae, and Rhopalidae within the superfamily, and Schaefer (1981) and Henry (1997a) supported the addition of the Hyalocephalidae and Stenocephalidae. Overall, the group is defined by the platelike ovipositor, the shortened buccula, and loss of the Y chromosome (Henry 1997a).

The Alydidae, or broad-headed bugs, are a relatively small group comprising about 45 genera and more than 254 species separated into two (Cassis and Gross 1995, Schuh and Slater 1995, Zoological Record 1996–2007) or, more recently, three subfamilies (Schaefer 1999a). Most are slender bugs with rather broad heads. Many, such as members of the genus *Alydus*, are strongly myrmecomorphic, especially in the nymphal stages. Schaefer and Mitchell (1983), in reviewing feeding habits, concluded that most Alydinae specialize on leguminous plants (Fabaceae), whereas most Leptocorisinae are grass (Poaceae) feeders. Wheeler and Henry's (1984) observations on the North American *Esperanza texana* Barber further supported Schaefer and Mitchell's (1983) speculation that micrelytrines specialize on grasses. Schaffner (1964) reviewed many of the alydine genera; Schaefer (e.g., 1996) and others (e.g., Schaefer and Ahmad 2007) have studied various other genera; Ahmad (1965) revised the Leptocorisinae of the world; and Schaefer (1999a) treated the higher classification.

The Coreidae (Figs. 10.43–10.45), often called leaf-footed bugs, pod bugs, or squash bugs based on relatively small groups of genera, are one of only two major families (the other being Pentatomidae) lacking a recent world catalog. The family contains about 267 genera and more than 1884 species worldwide (Schuh and Slater 1995, Zoological Record 1996–2007). Most recent authors have recognized three subfamilies (e.g., Packauskas 1994, Brailovsky and Cassis 1999, Cassis and Gross 2002), but the tribal classification is utterly confusing, ranging from 10 (Cassis and Gross 2002) to 30 tribes (Schuh and Slater 1995). Packauskas (1994) provided a key to the subfamilies and tribes of the Western Hemisphere; no similar treatment, however, is available for the Eastern Hemisphere. Of the three subfamilies, the Coreinae is by far the largest and contains most of the economically important species. In North America, *Leptoglossus phyllopus* (Linnaeus) is a serious pest of various crops (Mead 1971, Bolkan et al. 1984, Mitchell 2006). Species of the genus *Chelinidea* often become pests of ornamental and rangeland cacti (*Opuntia* spp.: Cactaceae), but several species, including *C. vittiger* Uhler, have been introduced into Australia to help control invasive prickly pear cacti (Dodd 1940). Species of the South Pacific genus *Amblypelta* can become severe pests of cacao, cassava, coconut, guava, and papaya (Mitchell 2000). The pseudophloeine tur pod bug *Clavigralla gibbosa* Spinola frequently causes serious injury or even total loss to various legumes, including pigeon pea, *Cajanus cajan*, in India (Dolling 1978). Schaefer and Mitchell (1983) reviewed the known host plants and Mitchell (2000) reviewed the economically important members of the family, as well as those used in biological control. Froeschner (1988b) cataloged the Nearctic fauna and Dolling (2006), the Palearctic.

The Rhopalidae (Figs. 10.46, 10.47), often called scentless plant bugs, are a small group ranging in length from about 4.0 to more than 15 mm. The common name is based on the greatly reduced ostiolar scent-gland opening. The family comprises about 21 genera and 209 species, separated into two subfamilies (Cassis and Gross 2002, Zoological Record 2003–2007). The Rhopalinae, containing six tribes, are mostly dull brown, punctate, pubescent bugs resembling certain small Coreidae or Lygaeidae (Orsillinae). The Serinethinae are usually brightly colored red and black, mostly glabrous bugs, frequently confused with lygaeine Lygaeidae. Most rhopalids are of little economic importance, but certain Serinethinae can become nuisance pests. In North America, the common boxelder bug, *Boisea trivittata* (Say), feeds on the seeds of boxelder, *Acer negundo*, and other trees of the maple family (Aceraceae). In the fall when the bugs seek overwintering shelter, they often invade homes in enormous numbers, leaving spots on furniture and other objects and giving off an offensive odor when crushed (Wheeler 1982, Henry 1988g). *Niesthrea louisianica* Sailer has been used in the biocontrol of velvet leaf, *Abutilon theophrasti* (Malvaceae) (Spencer 1988). Chopra (1967) studied the

higher classification and provided keys to the subfamilies, tribes, and genera, and Göllner-Scheiding (1983) cataloged the family for the world, including reference to several important generic revisions.

The Hyocephalidae, a small family restricted to Australia, is represented by only two genera and three species (Brailovsky 2002, Cassis and Gross 2002). Hyocephalids are relatively large (up to 15 mm long) bugs thought to feed on fallen seeds. They are characterized by the elongate, reddish-brown to black body and the possession of a glandular organ termed an external strainer or pore-bearing plate found laterally on abdominal sternum III (Štys 1964). They have their closest affinity to the Stenocephalidae (Schaefer 1981, Henry 1997a).

The family Stenocephalidae (Fig. 10.48) is represented by only one (*Dicranocephalus*) or two (*Psotilnus*) genera. The number of species has been somewhat controversial as well. Lansbury (1965, 1966) recognized two genera and 36 species, whereas Moulet (1995a, 1995b) considered only one genus and 16 valid species. These bugs are restricted to the Old World, with only one known from Australia. One species described from the Galapagos Islands, *D. insularis* Dallas, is now thought to be an Old World immigrant that was subsequently described as *D. bianchii* (Jakovlev 1902) based on specimens from its native range in northern Africa and southern Asia (Moulet 1995b, Henry and Wilson 2004). Henry and Wilson (2004) inadvertently used the junior synonymic name *D. bianchii* rather than *D. insularis*, the older name. Stenocephalids are elongate, subparallel bugs up to 15 mm long. They possess both coreoid (e.g., numerous hemelytral veins, four-lobed salivary gland) and lygaeoid (e.g., laciniate ovipositor, XY chromosome) characters (Henry 1997a).

Idiostoloidea

The Henicocoridae are represented by only one genus and one species, *Henicocoris monteithi* Woodward, restricted to southern Australia (Cassis and Gross 2002). Woodward (1968a) described the subfamily Henicocorinae for *H. monteithi* within the Lygaeidae *sensu lato*, and later, Henry (1997a) gave the group family status and formally established its sister-group relationship with the Idiostolidae.

The Idiostolidae are a small family of rhyparochromid like bugs comprising three genera and four species, one known only from Argentina and Chile and three from Australia (Woodward 1968b). Idiostolids, first included as a subfamily of the Lygaeidae *sensu lato* (Scudder 1962a), were given family status by Štys (1964). Apomorphic for these bugs are the numerous but short abdominal trichobothria and the absence of a spermatheca (Scudder 1962a, Henry 1997a). Idiostolids are associated with mosses in *Nothofagus* forests and most likely are phytophagous.

Lygaeoidea

The family classification within the Lygaeoidea has fluctuated considerably in recent years. Leston (1958) considered the Lygaeidae paraphyletic and suggested that it should be separated into at least five families. Štys (1967b) and Schaefer (1975), likewise, speculated on the paraphyly of the Lygaeidae and various relationships, particularly within the malcid line that included the Berytidae, Colobathristidae, Cyminae, and Malcidae. Henry (1997a) concluded that the Lygaeidae were polyphyletic and, as a consequence, transferred the Henicocorinae as a family to the Idiostoloidea, and gave family status to 10 subfamilies, forming a more broadly defined Lygaeoidea comprising 15 families. Slater (1964) and Slater and O'Donnell (1995) cataloged the Lygaeidae (*sensu lato*) for the world.

The Artheneidae are a mostly Palearctic group containing 8 genera and 20 species, previously separated into 4 subfamilies (Cassis and Gross 2002). Kerzhner (1997) gave evidence that the only New World representative of the family, *Polychisme poecilus* Spinola (Polychisminae), a position established by Slater and Brailovsky (1986), belongs in the Lygaeidae (*sensu stricto*) as a tribe of the Ischnorhynchinae. Artheneids are small, strongly punctate, oval bugs, with widely explanate, lateral pronotal carinae. Although naturally occurring only in the Old World, two immigrant species, *Chilacis typhae* (Perrin) (Wheeler and Fetter 1987) and *Holcocranum saturejae* (Kolenati) (Hoffman and Slater 1995) are now well established in North America (Wheeler 2002).

The Berytidae (Fig. 10.49), commonly referred to as stilt bugs because of the long, slender legs of most species, comprise 36 genera and 172 species, separated into 3 subfamilies and 6 tribes (Henry and Froeschner 1998, 2000; Henry 2000a, 2007; Kment and Henry 2008). Stilt bugs range in size from 2.3 mm for certain species of the New World genus *Pronotacantha* to more than 16 mm for *Plyapomus longus* Štusak,

known only from St. Helena. Most members of the Gampsocorinae and Metacanthinae have long, slender bodies, with even longer, thread-thin legs and antennae (Henry 1997b, 1997c); all species of *Hoplinus* are armed with stout spines on the head, pronotum, and, frequently, the hemelytra (Henry 2000a). Wheeler and Schaefer (1982) provided a world review of host plants, noting that most live on glandular-hairy or viscid plants, and Henry (2000b) reviewed their economic importance, highlighting both phytophagous and zoophagous feeding habits. Morkel (2006) documented kleptoparasitism by four European species, including the obligate associate *Metacanthus annulosus* (Fieber), in the funnel-webs of the spider *Agelena orientalis* Koch (Araneae: Agelenidae). Henry (1997b) provided a phylogenetic analysis and key to the genera of the world, Henry (1997c) monographed the family for the Western Hemisphere, and Henry and Froeschner (1998) provided a world catalog.

The Blissidae (Fig. 10.50), or chinch bugs, comprise about 50 genera and 435 species (Slater and O'Donnell 1995, Cassis and Gross 2002). All are restricted to feeding on monocots, especially Poaceae, and less commonly on Cyperaceae and Restionaceae (Slater 1976). Blissids are broadly oval to elongate, often flattened, and range in size from less than 3.0 mm to more than 15 mm. The family contains a number of serious crop and turf pests. The common chinch bug, *Blissus leucopterus* (Say), perhaps the most important species in the Lygaeoidea, is a major pest of turf grasses, corn, and cereal crops in North America (Sweet 2000a). Slater (1976) reviewed host plants and Sweet (2000a) provided a detailed overview of their economic importance. Slater (1979) monographed the group as a subfamily and Henry (1997a) elevated Blissinae to family status.

The Colobathristidae are a small group of tropical bugs ranging in length from about 6.0 mm to more than 20 mm. They comprise about 23 genera and 84 species separated into two subfamilies found mostly in the Oriental and Neotropical Regions (Schuh and Slater 1995). Colobathristids, characterized by their slender, elongate bodies and relatively long legs, possess characters appearing in part coreoid and lygaeoid. Henry (1997a) reaffirmed their position in the Lygaeoidea as the sister group of Berytidae. All species feed on grasses, and some are pests of sugarcane in Indonesia and Australia (Sweet 2000a). Horváth (1904) monographed the family and Carvalho and Costa (1989) provided a key to the Neotropical genera.

The Cryptorhamphidae, represented by only two genera and four species restricted to the Australian Region, are small yellowish-brown, punctate bugs, with dorsal spiracles (Henry 1997a, Cassis and Gross 2002). Previously placed in the Cyminae, the cryptorhamphids were placed by Hamid (1971) in their own subfamily, which Henry (1997a) elevated to family.

The Cymidae are small, yellowish-brown bugs, comprising about nine genera and 54 species that are most common in the Eastern Hemisphere (Cassis and Gross 2002). Hamid (1975) monographed the group as a subfamily and Henry (1997a) gave Cyminae family status. Cymids feed primarily on monocots, especially Cyperaceae (Hamid 1975, Péricart 1998).

The Geocoridae (Fig. 10.51), or big-eyed bugs, are a widespread group, comprising 25 genera and about 274 species, separated into three subfamilies (Henry 1997a, Cassis and Gross 2002, Zoological Record 2003–2007). They are characterized by their often enlarged kidney-shaped eyes, broad heads, and the posteriorly curved abdominal sutures between segments 4 and 5 and 5 and 6 (Readio and Sweet 1982, Henry 1997a). Most members of the subfamily Geocorinae are predatory and frequently used in biocontrol programs (Sweet 2000b). Many Pamphantinae are strongly myrmecomorphic, such as the genera *Cattarus* and *Cephalocattarus* (Slater and Henry 1999).

The Heterogastridae are primarily an Old World family, comprising 24 genera and 100 species (Cassis and Gross 2002, Zoological Record 2003–2007), with only two occurring in the Nearctic (Ashlock and Slater 1988). Henry (1997a) hypothesized a sister relationship with the Pachygronthinae based on the deeply inserted ovipositor and noninflatable vesica. Péricart (1998) associated several species with the plant families Lamiaceae and Urticaceae. Scudder (1962b) provided a key to the world genera.

The family Lygaeidae (*sensu stricto*) (Fig. 10.52) comprises about 102 genera and 968 species (Slater and O'Donnell 1995, Zoological Record 1996–2007), separated into three subfamilies: the Ischnorhynchinae, Lygaeinae, and Orsillinae (Henry 1997a). Lygaeids are best recognized by the impressed line across the calli, the Y-shaped pattern on the scutellum, and the dorsal position of abdominal spiracles II through VII. The Ishnorhynchinae comprise about 75 species of dull brown to reddish-brown bugs. The most widespread north temperate genus *Kleidocerys* contains the well-known and occasional nuisance pest, the birch catkin bug, *K. resedae* (Panzer) (Wheeler 1976b).

The Orsillinae, represented by about 250 species, contains the widespread pest genus *Nysius*, collectively often called false chinch bugs (Barber 1947, Péricart 1998). The Lygaeinae, with more than 500 species, are among the most recognized and well-studied Lygaeoidea. Many, such as the species of *Lygaeus*, *Oncopeltus*, and *Spilostethus*, are aposematically colored. Slater (1992) treated the New World fauna and Péricart (1998), the western Palearctic.

The Malcidae are dull, punctate bugs about 3.0 to 4.0 mm long, with waxy setae, stylate eyes, and spined or tuberculate immatures (Štys 1967b, Sweet and Schaefer 1985). Three genera and about 29 species are separated into two subfamilies, the Chauliopinae and Malcinae. The biology and hosts are largely unknown, but several species of *Chauliops* are pests of beans (Fabaceae) in Asia and India (Sweet 2000a).

The Ninidae are a small family represented by five genera and 13 species (Cassis and Gross 2002). They measure about 3.0 to 4.0 mm long and are characterized by their broad head, stylate eyes, often translucent or hyaline hemelytra, and the bifid apex of the scutellum (Henry 1997a). Previously included as a tribe of the Cyminae, the group was given family status by Henry (1997a). Scudder (1957) provided a world revision.

The Oxycarenidae comprise 23 genera and 147 species of primarily Eastern Hemisphere bugs (Cassis and Gross 2002). They are characterized by the punctate, porrect head, hyaline often explanate hemelytra, truncate female abdomen, and transverse comb of setae on the male abdomen (Henry 1997a). *Oxycarenus*, by far the largest genus, contains several economically important species (Sweet 2000a), including *O. hyalinipennis* (Costa) introduced into the New World tropics (Slater and Baranowski 1994). Samy (1969) revised the African fauna and Henry (1997a) gave the group family status.

The family Pachygronthidae (Fig. 10.53), containing 13 genera and 78 species, is separated into two subfamilies, the Pachygronthinae and Teracriinae (Cassis and Gross 2002). The pachygronthines are distinguished by the strongly incrassate, spined profemora and the unusually long first antennal segments. Teracriines have shorter antennae and are held together in the family based only on the ventral position of the abdominal spiracles (Henry 1997a). Members of the family feed primarily on monocots (Cassis and Gross 2002). Slater (1955) provided a world revision.

The Piesmatidae (Fig. 10.54), often called ash-gray plant bugs, were considered related to the Tingidae (Cimicomorpha) until Drake and Davis (1958) clarified their position within the Pentatomomorpha; Henry (1997a) gave further support for their placement in the Lygaeoidea. Six genera and about 44 species are separated into two subfamilies, the Piesmatinae and Psamminae (Henry 1997a, Cassis and Gross 2002). Drake and Davis (1958) revised the world genera and Heiss and Péricart (1983) treated the Palearctic fauna. Slater and Sweet (1965) discussed relationships within the Psamminae, and Henry (1997a) transferred the subfamily into the Piesmatidae based on numerous shared characters, including dorsal 'areoles', two-segmented tarsi, presence of trichobothrial pads, and the loss of certain abdominal trichobothria.

The Rhyparochromidae (Figs. 10.55, 10.56) represent the largest lygaeoid family with 372 genera and more than 1850 species, separated into two subfamilies, the Plinthisinae and Rhyparochrominae, and 14 tribes (Slater and O'Donnell 1995, Cassis and Gross 2002, Zoological Record 2003–2007). Cassis and Gross (2002) provided a table giving the number of genera and species for each tribe. Rhyparochromids are recognized by the incomplete abdominal suture between segments 4 and 5 (except Plinthisinae) and the presence of a trichbothrium near each eye (Henry 1997a). The five largest tribes – the Rhyparochromini (370 mostly Old World species), Myodochini (322 primarily Western Hemisphere species), Drymini (280 primarily North American and Eastern Hemisphere species), Ozophorini (175 largely New World and Oriental species), and Lethaeini (153 worldwide species) – represent more than 70% of the family. Nearly all Rhyparochrominae, with the exception of the haematophagous Cleradini, are seed feeders, thus, the common name seed bugs. Most taxa have enlarged forefemora for grasping seeds. Although most rhyparochromids are not considered major pests, several immigrant species can become serious nuisance pests in western North America, when they invade homes and other structures during outbreak populations (Henry and Adamski 1998, Henry 2004).

Pentatomoidea

This superfamily comprises 16 families. The last world pentatomoid catalog by Kirkaldy (1909) is long outdated. The more recent regional catalogs

include those of Henry and Froeschner (1988) for the Nearctic, with chapters by Froeschner; Cassis and Gross (2002), for Australia; and Aukema and Rieger (2006) for the Palearctic, with chapters by J. Davidová-Vilímová, U. Göllner-Scheiding, J. A. Lis, and D. A. Rider. D. A. Rider (personal communication) is working toward a world pentatomid catalog and maintains a website (Rider 2008) containing a list of genera, a comprehensive bibliography, and a wealth of other information pertaining to the Pentatomoidea.

The Acanthosomatidae (Fig. 10.57) are a small family comprising about 46 genera and 184 species, separated into three subfamilies (Cassis and Gross 2002; Froeschner 1997, 2000, Zoological Record 2003–2007). Acanthosomatids are characterized by a combination of two-segmented tarsi, hidden spiracles on the second abdominal segment, paired trichobothria on abdominal segments III–VII, a large mesosternal keel, an anteriorly directed spine on abdominal segment III, and a large exposed eighth abdominal segment in males (Kumar 1974). Most species are found in north temperate regions or at higher elevations in the subtropics (Thomas 1991). Females possess paired abdominal structures known as Pendergrast's organs and exhibit strong maternal brooding behavior (Tallamy and Schaefer 1997). Kumar (1974) provided a world revision with keys to subfamilies, tribes, and genera; Thomas (1991) revised the North American fauna.

The Aphylidae, consisting of only two genera and three species, are restricted to the Australian Region. They are 4–5 mm long and characterized by a strongly convex, oval shape, large 'scutellerid-like' scutellum, and long labium extending beyond the metacoxae. Although Gross (1975) and Rider (personal communication in Cassis and Gross 2002) considered aphylids aberrant pentatomids, Schuh and Slater (1995) and Cassis and Gross (2002) maintained their family status. Štys and Davidová-Vilímová (2001) provided the most recent family review, including the description of a new genus and one new species.

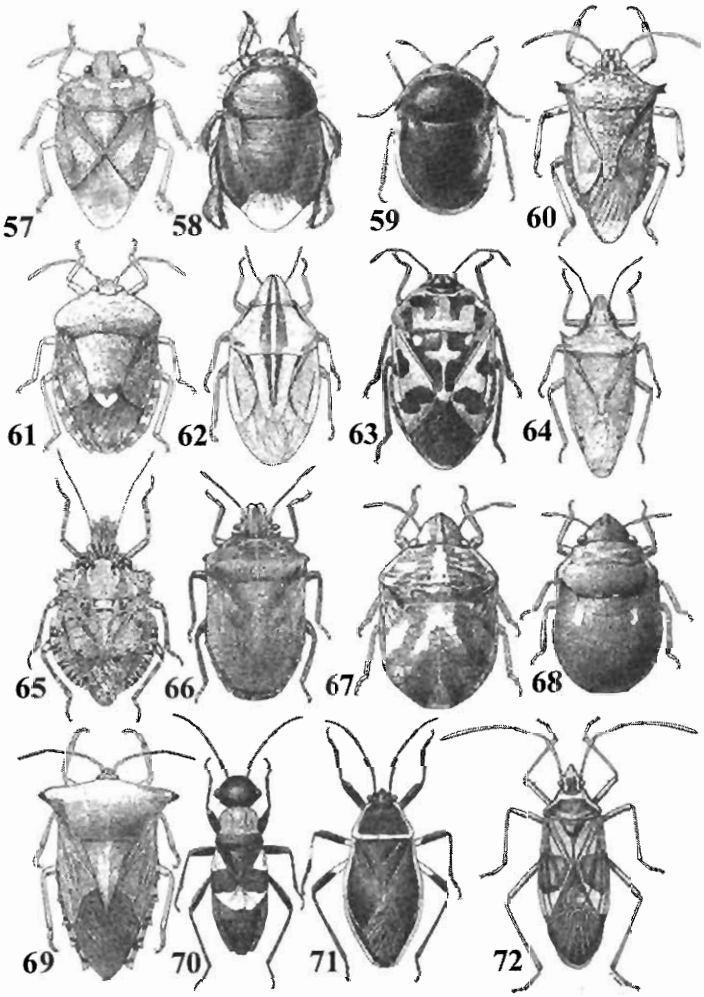
The Canopidae are small, round, convex pentatomoids represented by only one genus and eight species in the New World tropics (Schuh and Slater 1995). McAtee and Malloch (1928) revised the group and McDonald (1979) studied the male and female genitalia of several species. McHugh (1994) associated nymphs and adults of two species, *Canopus burmeisteri* McAtee and Malloch and *C. fabricii* McAtee and Malloch, with polypore fungi on rotting logs.

The Cydnidae (Figs. 10.58, 10.59), or burrowing bugs, are a worldwide group of about 120 genera and 765 species, separated into five (Froeschner 1960) to seven subfamilies (Lis 2006), including the Corimelaeninae and Thyreocorinae (Schuh and Slater 1995, Cassis and Gross 2002, Zoological Record 2003–2007; but see Lis 2006). Burrowing bugs range in size from about 2 to 20 mm and are characterized by their round to oval shape, brown to black coloration, and often spiny legs modified for digging in soil. Many cydnids feed on the roots of their hosts, but members of the subfamily Sehirinae feed on plants like most Pentatomidae (Froeschner 1988c). Most species are of little economic importance, but occasionally they become abundant and cause serious injury to crops (Froeschner 1988c, Lis et al. 2000). Froeschner (1960) monographed the Cydnidae of the Western Hemisphere and J. A. Lis (1999) cataloged the Old World fauna and since (e.g., Lis 2000, 2001) has revised numerous genera. Lis et al. (2000) reviewed the economically important species.

The Cyrtocoridae are a small New World group of pentatomoids 6–10 mm long. They are characterized by the oval, strongly convex form, tuberculate scutellum, explanate connexival segments, and scalelike setae (Packauskas and Schaefer 1998). Formerly treated as a subfamily of the Pentatomidae (e.g., Schuh and Slater 1995), the group was accorded family status by Packauskas and Schaefer (1998), who presented keys to the four genera and eleven species. At least one species feeds on leguminous plants (Fabaceae) (Schaefer et al. 2000).

The Dinidoridae, primarily Oriental and Afrotropical, comprise only 16 genera and 65 species, separated into two subfamilies (Rolston et al. 1996). Most species are thought to be phytophagous, with several becoming pests of certain cucurbits (Schaefer et al. 2000). They are 9–27 mm in length and characterized by large, stout bodies, a short scutellum, and keeled heads (Schuh and Slater 1995). Durai (1987) revised the family and Rolston et al. (1996) cataloged the world fauna.

The Australian family Lestoniidae comprises one genus and only two species (McDonald 1969). These round convex bugs, resembling certain tortoise beetles (Chrysomelidae) and measuring from about 3.5 mm to nearly 6.0 mm long, apparently are related to Plataspidae (China and Miller 1959, Schaefer 1993). *Lestonia haustorifera* China feeds on species of Australian



Figs. 10.57–10.72 Pentatomomorpha. 10.57, *Rolstonus rolstoni* Froeschner [Acanthosomatidae: Pentatomoidea]; 10.58, *Scaptocoris castaneus* Perty [Cephalocteinae: Cydnidae: Pentatomoidea]; 10.59, *Corimelaena pulicaria* (Germar) [Thyreocorinae: Cydnidae: Pentatomoidea]; 10.60, *Alcaeorrhynchus grandis* (Dallas) [Asopinae: Pentatomidae: Pentatomoidea]; 10.61, *Edessa florida* Barber [Edessinae: Pentatomidae: Pentatomoidea]; 10.62, *Aelia americana* Dallas [Pentatominae: Pentatomidae: Pentatomoidea]; 10.63, *Murgantia histrionica* (Hahn) [Pentatominae: Pentatomidae: Pentatomoidea], 10.64, *Oebalus pugnax* (Fabricius) [Pentatominae: Pentatomidae: Pentatomoidea]; 10.65, *Parabrochymena arborea* (Say) [Pentatominae: Pentatomidae: Pentatomoidea]; 10.66, *Amaurochrous cinctipes* (Say) [Podopinae: Pentatomidae: Pentatomoidea]; 10.67, *Camirus porosus* (Germar) [Scutelleridae: Pentatomoidea]; 10.68, *Sphyrocoris obliquus* (Germar) [Scutelleridae: Pentatomoidea]; 10.69, *Piezosternum subulatum* (Thunberg) [Tessaratomidae: Pentatomoidea]; 10.70, *Arhaphe carolina* Herrich-Schaeffer [Largidae: Pyrrhocoroidea]; 10.71, *Largus succinctus* (Linnaeus) [Largidae: Pyrrhocoroidea]; 10.72, *Dysdercus lunulatus* Uhler [Pyrrhocoridae: Pyrrhocoroidea]. (Fig. 10.57 after Froeschner 1997; 10.58–10.69, Froeschner 1941; 10.70, 10.71, Froeschner 1944; 10.72, Froeschner 1985).

cypress, *Callitris* spp. (Cupressaceae) (McDonald 1970, Cassis and Gross 2002).

The Megarididae are a small Neotropical family of round, strongly convex bugs with a large globose scutellum covering the wings and abdomen. They are represented by only one genus, *Megaris*, and 16 species (McAtee and Malloch 1928), all of which are about 5.0 mm or less in length. Previously considered a subfamily of the Pentatomidae, megaridids have been given family status (McDonald 1979), but their relationship to other families remains unclear (Schuh and Slater 1995).

The Parastrachiidae, containing only one genus and two Oriental and eastern Palearctic species, until recently, were placed as a tribe of the Pentatomidae or a subfamily of the Cydnidae (Schaefer et al. 1988). Sweet and Schaefer (2002), based on wing morphology, scent-gland structure, and male and female genitalia, elevated the group to family status. Parastrachiids are bright red and black bugs, 15–18 mm long. They exhibit subsocial behavior (Tallamy and Schaefer 1997) and maternal egg guarding (Miyamoto 1956).

The family Pentatomidae (Figs. 10.60–10.66), often called stink bugs, is the largest heteropteran group that lacks a modern world catalog. Stink bugs are recognized by the oval body, 4- or 5-segmented antenna, entire hemelytra with 5–12 veins, and 2- or 3-segmented tarsi. Approximately 900 genera and 4700 species

are separated into eight or nine subfamilies (Cassis and Gross 2002, Rider 2008). The predatory subfamily Asopinae (Fig. 10.60), with approximately 63 genera and more than 350 species, contains some of the most important biocontrol agents used in agricultural ecosystems, including members of the New World genus *Podisus* (McPherson 1982, De Clercq 2002). Thomas (1992) revised the New World fauna and gave a synopsis of the Old World genera (Thomas 1994). The largest subfamily, Pentatominae (Figs. 10.61–10.65), is represented by more than 404 genera and 2771 species (Schuh and Slater 1995). Among its members are a large number of economically important species, including the Palearctic *Aelia furcula* Fieber, a pest of small grains; the Australian spined citrus bug, *Biprorulus bibax* Breddin; the widespread 'southern green stink bug', *Nezara viridula* (Linnaeus); and New World species of the genus *Euschistus*, which attack various agricultural crops (McPherson 1982, McPherson and McPherson 2000, Panizzi et al. 2000). The Nearctic fauna has been cataloged by Froeschner (1988d), the Australian by Cassis and Gross (2002), and the Palearctic by Rider (2006a).

The Phloeidae are large (20 to 30 mm), mottled brown, flattened bugs with strongly expanded lateral plates around the body, and a color and shape that make them well camouflaged against the lichen-covered bark of their host trees (Lent and Jurberg 1965, 1966). Only two genera and three species are known. The strongly foliate body margins, the three-segmented antenna, and the unique male genitalia distinguish them from all other pentatomoids (Lent and Jurberg 1965, Schuh and Slater 1995). Phloeids exhibit strong maternal egg care and, upon hatching, early instars attach to the undersurface of the female for protection. When disturbed, these bugs emit a stream of clear liquid from the anal opening (Hussey 1934).

The Plataspidae are an Eastern Hemisphere group, most abundant in the Oriental Region. They measure 2–20 mm long and are characterized by their round, strongly convex bodies and large scutellum that covers the abdomen and hemelytra. Fifty-nine genera and about 560 species are known (Jessop 1983, Davidová-Vilímová 2006). All plataspids are phytophagous, with most specializing on leguminous plants (Fabaceae) (Schaefer 1988). Most records of economic damage to various crops pertain to species of the largest genus *Comptosoma*, with 280 species (Schaefer et al. 2000). Jessop (1983) reviewed and provided keys to the genera of the *Libyaspis* group and provided a checklist of the species; Davidová-Vilímová (2006) cataloged the Palearctic fauna.

The Scutelleridae (Figs. 10.67, 10.68), or shield bugs, are represented by 81 genera and about 450 species, separated into six subfamilies (Schuh and Slater 1995, Göllner-Scheiding 2006). Shield bugs, measuring from about 5.0 to 20.0 mm long, are distinguished by the oval, often convex shape and large scutellum that covers the abdomen and most of the hemelytra. Most scutellerids are dull mottled brown or gray, but many members of the Scutellerinae are brightly colored and often iridescent (Javahery et al. 2000), making them some of the most spectacularly colored of all Heteroptera (Schuh and Slater 1995). Cassis and Vanags (2006) revised the 13 genera and 25 species of Australian jewel bugs. By far the most economically important species is the Sunn pest, *Eurygaster integriceps* Puton, which often devastates wheat and other small grain crops in Asia and the Middle East (Javahery et al. 2000).

The Tessaratomidae (Fig. 10.69) comprise 55 genera and 240 species, separated into three subfamilies (Rolston et al. 1994, Rider 2006b). Most occur in the Old World, with only three species in the Neotropics. Tessaratomids are large robust bugs, some more than 40 mm long. In addition to their large size, they are characterized by the proportionately small head, short labium, and large sternal plate between the middle and hind coxae. The bronze orange bug, *Musgraveia sulciventris* Stål, is the most serious pest in the family, causing economic injury to citrus in Australia. Rolston et al. (1994) cataloged the family. Sinclair (2000) revised the genera of Oncomerinae. Cassis and Gross (2002) cataloged the Australian fauna and Rider (2006b) the Palearctic.

The Thaumastellidae are small, enigmatic bugs, 3.5 mm or less in length, found only in the Afrotropical Region and the Middle East (Schuh and Slater 1995). Only one genus and three species are known. Though they are clearly related to the Cydnidae (Dolling 1981), Jacobs (1989) maintained them as a family. Thaumastellids occur under rocks, where they apparently feed on fallen seeds (Jacobs 1989).

The Urostylididae, comprising 11 genera and about 170 species, are found mostly in southern and eastern Asia (Rider 2006c). They are elongate-oval bugs, with proportionately small heads and long antennae, measuring about 3.5 to 14.0 mm in length. (Schuh and Slater 1995). Rider (2006c) summarized the

taxonomic literature and cataloged the Palearctic fauna; Schaefer et al. (2000) reviewed the economic species.

Pyrrhocoroidea

Henry (1997a) reviewed the classification and considered the Pyrrhocoroidea, containing only two families, the sister group of the Coreoidea.

The Largidae (Figs. 10.70, 10.71) are a small, worldwide group, containing 13 genera and about 106 species, separated into two subfamilies, the Larginae and Physopeltinae (Schaefer 2000, Cassis and Gross 2002, Zoological Record 2003–2007). Largids are medium to large (more than 50 mm), often brightly colored bugs, characterized by the lack of ocelli, four-segmented labium and antenna, seven to eight veins on the membrane arising from two closed basal cells, and sometimes fused abdominal segments (Henry 1988d, 1997a; Schuh and Slater 1995). All are phytophagous (Schaefer and Ahmad 2000). The New World subfamily Larginae is separated into two tribes, the Araphini (Fig. 10.70) and Largini (Fig. 10.71) (Schaefer 2000). The former comprises largely the genus *Largus* and the latter, several strongly myrmecomorphic genera, including *Araphe* and *Pararaphe* (Henry 1988d). The Physopeltinae, restricted to the Old World, are large, mostly red, aposematically colored bugs. Hussey (1929) cataloged the world fauna. More recently, Henry (1988d) cataloged the Nearctic, Kerzhner (2001) the Palearctic, and Cassis and Gross (2002) the Australian Region.

The Pyrrhocoridae (Fig. 10.72), or cotton stainers, are represented by about 33 genera and 340 species (Kerzhner 2001, Zoological Record 2003–2007). Pyrrhocorids are medium-sized to large bugs, from about 8.0 to more than 30.0 mm long, and usually aposematically colored red, yellow, and white. They are distinguished by the lack of ocelli, a reduced metathoracic scent-gland opening, two closed cells at the base of the wing membrane, and a platelike ovipositor (Henry 1988f, 1997a, Schuh and Slater 1995). *Dysdercus*, by far the largest genus, occurs nearly worldwide and contains several important cotton pests that cause damage directly by feeding on cotton bolls, and indirectly by introducing bacteria and fungi that cause the bolls to rot (Whitefield 1933, Schaefer and Ahmad 2000). Freeman (1947) treated many of the Old World species and Doesberg (1968) revised the New World fauna. Several members of the genera *Antilochus* and *Raxa* are facultatively predaceous, sometimes becoming obligate predators (Schaefer 1999b).

THE IMPORTANCE OF HETEROPTERAN BIODIVERSITY

Although it is well documented that insects are the most diverse group of organisms, comprising more than half the described species, we are far from knowing the exact number coexisting with us on earth. With Hemiptera considered the fifth largest order, and the suborder Heteroptera containing nearly half of the estimated 90,000 species (Cassis et al. 2006), this diverse group, exhibiting both phytophagous and zoophagous feeding habits (Schuh and Slater 1995), affects nearly every aspect of our environment. The pursuit of a better understanding of true bug diversity, therefore, is paramount. Taxonomy and systematics, as hypothesis-driven disciplines (Wheeler 2004), form the foundation for all biological research through the predictive value they impart from taxon-based studies. For example, newly discovered predatory species related to known beneficial taxa can be expected to have similar biological control potential. If the 10,000 species described during the past 250 years (1758 to present) represent only half the number of Miridae that eventually will be discovered (Henry and Wheeler 1988), an enormous amount of important biological, biogeographic, and host information useful to other disciplines remains to be discovered. Considering the previous rate of only 40 species described per year, the concept of an 'industrialized' effort to combine the global resources of multiple scientists and students, modern technology, and extensive fieldwork in hot-spot areas made possible only through large-scale funding (Cassis et al. 2006) takes on new merit.

That billions of dollars worth of losses to crops are caused by Heteroptera each year reflects, perhaps, the single most important reason to study this diverse suborder. Throughout this chapter, I have given examples of the many true bug attributes, including information on their morphology, distribution, numbers, host associations, and economic importance. The Heteroptera fall primarily into two broad feeding regimes, plant feeders and predators (Schaefer and Panizzi 2000, A. Wheeler 2000a, 2000b, 2001), with

many intermediate variations. As a consequence of globalization, greater numbers of true bugs are being transported beyond their native ranges through international commerce, creating new pest situations in foreign lands (Wheeler and Hoebeke 2008), many times involving taxa previously unknown to science (e.g., Dolling 1972). Recent treatments of various families, such as the Coreidae (Mitchell 2000), Lygaeoidea (Sweet 2000a), Miridae (Wheeler 2000a, 2001), Pentatomidae (McPherson and McPherson 2000), and other families presented in Schaefer and Panizzi (2000), have provided much-needed synthesis of widely scattered information important to better understanding certain pest groups.

The effect of global warming on heteropteran distribution also is being reflected through various studies. In eastern North America, the rhopalid, *Jadera haematoloma* (Herrich-Schaeffer), has shown rapid northward dispersal in recent years (Hoffman and Steiner 2005). In Japan, rising temperatures have allowed the poleward range expansion of several rice and fruit-feeding Pentatomidae (Kiritani 2007). Musolin (2007) documented the northern movement of the southern green stink bug, *Nezara viridula* (Linnaeus), in central Japan since the 1960s. The incidence of vector-borne diseases can be affected as well. For example, rising temperatures can expand distributions, accelerate life cycle times, and increase population densities of certain species, as seen in some species of *Triatoma* (Reduviidae) that are vectors of *Trypanosoma cruzi*, the causal agent of Chagas's disease (Curto de Casas and Carcavallo 1995).

Although in most studies the phytophagous bugs are emphasized as agricultural pests, many heteropterans, including all of the Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, and most Cimicomorpha (excepting certain Miridae and all Tingidae), are exclusively or, in large part, predatory and are usually considered beneficial in agricultural situations. From a biological control viewpoint, the families Anthocoridae (*sensu lato*) (Lattin 2000), Geocoridae (Sweet 2000b), Miridae (Wheeler 2000b, 2001), Nabidae (Braman 2000), asopine Pentatomidae (De Clercq 2002), and Reduviidae (Ambrose 2000) contain the most important predatory species. Within these groups are also several external parasitic lineages that feed on vertebrate blood, including the Cimicidae, Polyctenidae, triatomine Reduviidae, and the rhyparochromid tribe Cleradini. Many aquatic bugs are well known for their value in mosquito control or as a food source for fish and other organisms (Menke 1979).

The Heteroptera are also important in conservation biology. The aquatic and semiaquatic bugs (Gerromorpha, Nepomorpha, and Leptopodomorpha) are well known for their role as water-quality indicators (Jansson 1987). Wheeler (2001) noted that certain Miridae might be of interest to conservation biologists as rare or unique species needing preservation, or as indicators of vitality or changes in ecosystems. For example, the type locality of the poorly known phlox-feeding plant bug, *Polymerus wheeleri* Henry, found in only 12 of 79 eastern US shale barren habitats, has essentially been destroyed by construction (Wheeler 1995, Henry, personal observations). Other rare species, such as the North Amerian *Corixidea major* McAtee and Malloch (Schizopteridae) known from only the holotype and two recent specimens taken in pine barren habitats (Hoffman et al. 2005), serve as valuable indicators of areas needing protection. Aukema (1994) concluded that the preservation and restoration of unique habitats should be made to protect populations of rare and endangered species in the Netherlands.

The overall influence of the Heteroptera as part of the fifth largest insect order is significant. Their roles as plant feeders, bloodsucking parasites, invertebrate predators, or water-quality indicators, make them unquestionably important organisms in our environment. More recent studies addressing the impact of global warming and the influence of Heteroptera in conservation biology reinforce the need for additional study. If even the lowest estimates of the number of Heteroptera prove accurate (Cassis et al. 2006), much challenging work remains to better understand this taxonomically complex and economically important group of fascinating insects.

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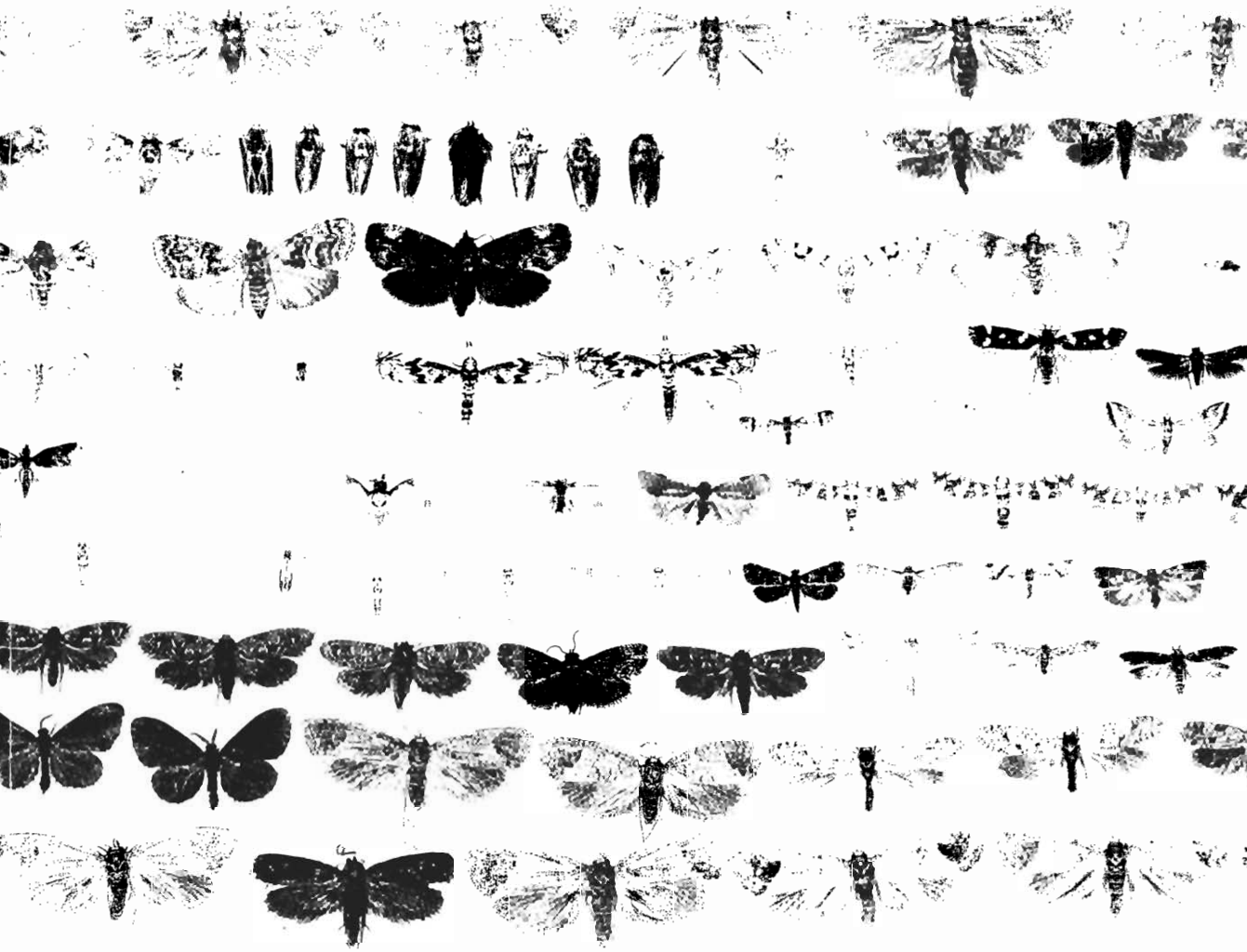

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